A CONTRIBUTION TO THE COMPARATIVE MORPHOLOGY OF THE THORACIC SCLERITES OF INSECTS.

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Although the thoracic sclerites are much used factors in insect classification and myology, there exists a most confusing lack of uniformity in the homologizing and terminology employed by the various writers upon these subjects. This confusion, it would appear has largely arisen from the fact that each investigator has been content to confine his attention to one or two groups of insects, applying his own terminology as occasion arose, or, more frequently, naming the sclerites without sufficient comparison with intermediate forms to determine their true homologies.

As would be naturally expected, many new and important points have been brought to light in each of the orders, but they stand as isolated facts, rather than as generalities applying to the Hexapoda as a whole. It is with the purpose of applying this knowledge to insects in general that a comparative morphological study has been here attempted.

MATERIAL.

The insects for study were collected in the United States, Europe and North Africa. With these I was able, through the kindness of Prof. R. Heymons, to compare a number of rare specimens in the Berlin Museum, not otherwise accessible. However, in so far as was possible, the commonest insects have been chosen to illustrate the types discussed, in order that any one wishing to verify the results might have no difficulty in procuring the necessary material.

TECHNIQUE.

The binocular microscope was found indispensable to the performing of dissections, which were always made and studied under a liquid medium, the rays of an artificial light being concentrated upon the object by means of a bull's-eye condenser. Glycerine or oil proved to be the most favorable medium for the examining of small objects, since they more readily remain in the position in which they are placed, when a denser medium is used.

In studying the musculature to determine the homology of the
sclerites, the so-called "Halbierungs methode" was largely employed.
Usually a series of dissections was prepared, in each case an additional
layer of muscles being removed, beginning at the mesal surface of
the bisected insect. The preparations thus made were fastened upon
thin strips of mica, by means of photoxylin, and preserved in 80%
alcohol. Since both mica and photoxylin are transparent, the speci-
men may thus be easily studied from either side.

Only in the case of very small insects, or when it was difficult to
follow the course of certain muscles, was it necessary to have recourse
to reconstructions from microtome sections.

In dealing with strongly chitinized material, good preparations
could be obtained only by the celloidin-paraffin embedding method,
and even then it was frequently necessary to paint the upper face of
the block with a thin film of mastix collodion before cutting each
section.

For general purposes, staining with Grenacher's hæmotoxylin,
differentiating with picric acid, and counterstaining with eosin gave
good results.

LITERATURE.

The works of Swammerdam, Linné, and all authors before Illiger's
time have but little interest other than from an historic point of view.
On the other hand such of the later publications as those of Chabrier,
'20; Strauss-Dürkheim, '28; Kirby and Spence, '28; Westwood, '39;
Burmeister, '32, etc., although very thorough and painstaking, are
too confusingly varied in their homologizing and terminology to have
any very great practical worth.

The most scientific handling of the subject is to be found in the
work of Audouin, '24, upon whose researches the modern terminology
is based. Since the appearance of this article, but little has been
added to our knowledge of the comparative morphology of the thorax.

Of the more modern publications the following were found very
useful in the preparation of this paper: For the homologizing of the
sclerites, Kleuker, '83; Kolbe, '93; Brauer, '88; Amans, '85; Börner,
'03; Verhoeff, '03; Janet, '98; Comstock, '02; Walton, '00, and Voss,
'04. For the terminology of the musculature, Luks, '83; Petri, '99;
Breed, '03; Voss, '04, and Durken, '07. For the wing venation, Adolph,
'80; Redtenbacher, '86; Comstock, '98, and MacGillivray, '06.

Such of the works as are of a more particular interest will be dis-
cussed under those headings to which they especially refer.

TERMINOLOGY.

The modern terminology for the thoracic sclerites is based upon the epoch-making work of Audouin, '20. Discarding the then prevalent conception of a binary division of the thorax according to the function of its organs of locomotion (as, for example, the collum and pectus of Knoch, 1801, the corselet and segment alifère of Chabrier, '20, or the mani- and ali-truncus of Kirby, '28) this author demonstrated that the thorax is composed of three similar segments. These three he designated as the pro-, meso-, and meta-thorax—terms variously attributed to Kirby, Latreille and Audouin, but which appear to have been first proposed by Nitzsch, '18. Nitzsch, however, used the slightly different form protothorax instead of prothorax.

Each segment Audouin considered as composed of four regions, namely, a dorsal region or tergum, two flanks or "pleuræ," and a ventral region called the sternum. The sternum he regarded as consisting of a single piece, but for the flanks and tergum he described a number of subdivisions.

In the flank or "pleura," he recognized the following parts: two large lateral plates, the anterior of which he termed the episternum, and the posterior the epimeron; a narrow strip along the anterior margin of the episternum called the parapleuron; a small plate containing the spiracle, called the peritreme; and a triangular sclerite articulating with the coxa, called the trochantine.

The tergum he considered as composed of four regions, lying one behind the other. Beginning with the most anterior he termed these the præscutum, scutum, scutellum and postscutellum.

Some entomologists employ the word dorsum to designate the tergal region of a single segment, but it is far preferable, as Audouin has done, to apply this term to the whole dorsal surface of the insect.

The expression stigma is frequently used as synonymous with spiracle, especially in the German publications; but, as used by systematists, the word stigma denotes the chitinized cell in the costal region of the wings of certain Hymenoptera, etc. It would, therefore, be preferable to use only the more exact and suitable term spiracle to denote the tracheal opening.

In most of the modern works there is a very great laxity in the use of the singular and the plural form of the word pleura. For example, some authors speak of one flank as the pleuron and both together as the pleura, while others, following Audouin's example, choose the latinized forms pleura and pleuræ. One cannot employ the term pleura in both a singular and plural sense without creating confusion,

and as the words are of Greek origin it would seem advisable to use only the etymologically correct forms, pleuron and pleura.

Recently the terms tergite, pleurite and sternite have been used interchangeably with tergum, pleuron and sternum. One form of the word appears to be amply sufficient for all ordinary purposes, and it would be far more practical to use the term tergite for a subdivision of the tergum, pleurite for a part of the pleuron, and sternite for a sclerite of the sternum. Thus the præscutum, scutum, etc., would be tergites, the epimeron and episternum pleurites, and so on. It is in this sense that these terms have been used in the text.

THEORETICAL DISCUSSION.

Before taking up the subdivisions of the segments in detail, a brief review of the theories dealing with the formation of the thorax will serve to give a clearer idea of the nature of the sclerites.

Despite Newport's, '39, statement to the contrary, Audouin seems to have regarded the thorax as consisting of but three simple segments. MacLeay, '30, however, and after him Newport, '39, proposed that each of the pro-, meso-, and meta-thoracic segments is in reality composed of four subsegments or annuli, which have become more or less completely fused together in the formation of the compact, highly specialized thorax. The præscutum, scutum, scutellum and post-scutellum, according to this theory, are the tergal portions of the four annuli, which are more closely fused in the pleural region and completely consolidated in the sternal region.

Hagen, '89, on the other hand, holds the view that each segment is composed not of four, but of three subsegments, each bearing a characteristic appendage. The most anterior he terms the leg-bearing, the next following the wing-bearing, and the last the spiracle-bearing subsegment.

The more modern theories are founded upon the work of Patten, '90, who claims that the thoracic segments are composed of but two annuli. From a comparison with the nervous system of Scolopendra, which he takes as a type, he concludes that in all Anthropoda the neuromeres, and consequently the segments themselves, are in reality double. In support of this view, he states that "in all anthropods carefully studied two cross commissures have been found in each neuromere," thus indicating the double nature of these structures. Furthermore, "in *Acilius* the median furrow between the cross commissures is similar to that found between the successive neuromeres." "In *Scorpio* the neuromeres are distinctly double," and in such forms

as *Julus* not only the neuromeres, but also the cardiac ostia, arteries, tracheæ and legs plainly show the double nature of the somites. Other indications of segmental fusion are two pairs of tracheal invaginations in each segment of *Acilius*, the bifurcated appendages of many Crustacea, and the bifid maxillæ of insects, in which latter group monsters with double pairs of legs are of frequent occurrence.

All of the subsequent theories, though differing greatly in their point of view, lay great stress upon the fusion of segments traceable in the Myriopoda as an indication of what has taken place in the Hexapoda.

Banks, '93, regards the suture between the episternum and epimeron as the boundary between two leg-bearing subsegments. Of these, the anterior or episternal subsegment, has retained its appendage fully developed, while the leg of the posterior or epimeral subsegment occurs only in a vestigial condition (the so-called styli found on the meso-, and meta-thorax of *Machilis* and other insects) or is completely fused with the episternal leg.

Walton's, '00–'01, theory differs from that of Banks only in the fact that he regards the epimeral leg as represented by the so-called meron or posterior portion of the coxa, and in that he believes that each sub-segment originally bore a wing. According to this author, only the epimeral wing is fully developed, while that of the episternal subsegment exists only as a wing "fundament," and is represented by the squamulæ, tegulæ, etc., designated under the common term pterygoda.

Kolbe, '93, whose book appeared contemporaneously with Banks', '93, first publication, differs from Banks and Walton, in regarding the epimeron and episternum as parts of the same segment, and in addition he finds traces of other "complementary" segments in such forms as *Locusta, Œdipoda*, etc. These complementary segments are especially well developed in the larvæ of *Lampyris*, and here show a great similarity to the condition found in *Scolopendrella*—which Kolbe considers as an intermediate form between the rest of the myriopods and insects.

Verhoeff, '02–'04, accepted Kolbe's theory, which he enlarged and worked out more in detail. Believing that traces of three "Vorder-segmente" or complementary segments (one in front of the pro-, meso-, and meta-thorax respectively) are to be found in such insects as *Japyx, Embia*, etc., he proposes that the typical hexapod thorax is composed of six primitive segments. To the "Vordersegmente" he gives the names micro-, steno- and crypto-thorax. Of these, the microthorax (the complementary segment in front of the prothorax) is the best developed, and occurs in a large number of insects. In

Japyx, etc., between each chief segment and its corresponding "Vorder-segment," and also in front of each Vordersegment, are found certain minute sclerites which Verhoeff interprets as the remains of two "intercalary" segments. Under these conditions, each of the three commonly accepted thoracic regions would in reality be composed of four subsegments (*i.e.*, a chief and a complementary segment, each with its corresponding intercalary segment), thus giving a total of twelve subsegments for the thorax as a whole.

In this connection it may be remarked that Banks, '04, is entirely incorrect in stating that his theory is supported by the views of Verhoeff. In reality the two are not at all alike, for, while Banks considers that the epimeron and episternum represent two annuli, Verhoeff expressly states that these two sclerites are parts of one and the same segment, in front of which he finds the additional so-called complementary and intercalary segments.

If then, with Banks, we consider the epimeron and episternum as representing two subsegments, a combination of Banks' and Verhoeff's theories would give five subsegments in each thoracic region, or a total of fifteen for the entire thorax. On the other hand, if MacLeay's, '30, contention, that the præscutum, scutum, scutellum and postscutellum represent four annuli, be correct, a combination of this with Verhoeff's theory would raise the total number of thoracic subsegments to twenty-one. This *reductio ad absurdum* only serves to show to what extremes it may lead if we regard each of the sclerites which chance to be serially arranged as the remains of a vestigial segment. Then, too, in view of the marked tendency toward the formation of separate chitinous plates which, as will be later discussed, takes place largely through mechanical causes, and for the most part without reference to any segmental arrangement, one cannot be too cautious in attributing to them a segmental value.

While it must be admitted that the "compound-segment" theory is a most attractive and not wholly groundless one, the following serious objections to the above cited theories may be made. Thus, the mere occurrence of four regions in the tergum, or the fact that the pleuron is divided into epimeron and episternum, is not sufficient proof that the segment is compound, since such divisions frequently occur from purely mechanical causes, and wholly without reference to any segmental arrangement—as, for example, the division of each segment into tergum, pleura and sternum.

Again, one should not lay too great stress upon the conditions found in Myriopoda as an indication of what has occurred in Insecta. A

similar mode of life frequently leads to a remarkable convergence in structure, which would, however, have no value in a genetic homologization. Furthermore, it must be borne in mind that insects are not descended from myriopods, but that recent Myriopoda, Crustacea, Insecta, etc., are groups of equal rank; and modifications in any direction may occur in each of the groups, quite independently of what occurs in any of the others.

Patten's argument, that the presence of two cross commissures in each neuromere is indicative of its double nature, loses its force when we consider that in many insects the last abdominal ganglion—which is regarded as the fusion product of a number of neuromeres—likewise contains but two cross commissures; whereas, if Patten's argument were correct, there should be as many commissures present as there are neuromeres entering into its composition. With regard to the bifurcated maxillæ of insects, it would appear far more reasonable to explain this condition as a secondary development, rather than the persistence of a primitive condition in such highly specialized appendages as the mouth parts; and Patten's other argument, that insect abnormalities with double pairs of legs are of frequent occurrence, has no weight when one considers the fact that there are likewise many vertebrate monsters with double appendages—yet no one considers this as a reversion to the primitive condition.

With regard to Kolbe's, '93, conclusions based upon the thorax of the larva of *Lampyris*, etc., it must be remembered that the larval form by no means represents the most primitive condition, but is rather an adaptation to its mode of life, as is so well shown in the hypermetamorphosis of *Sitaris humeralis*. Again, in certain lepidopteran larvæ—*Sphinx* for example—it is very easy to observe a marked tendency toward the formation of intrasegmental rings; and this suggests that the extra constrictions in the soft larval bodies of *Lampyris*, *Rhaphidia*, etc., are probably some such superficial modifications, especially since no indications of any subdivision is indicated in such important segmental structures as the ganglia, tracheæ, etc.

Banks', '93, theory, that the meso- and metathoracic styli of *Machilis* are rudimentary legs, has no support either from an embryological or a structural point of view, and he seems to have been unaware of Haase's, '89, far more probable explanation of these structures as modified setæ. Furthermore, Börner, '03, and Henneguy, '04, recently homologize these organs with the exopodite of the Crustacea, while Verhoeff, '03–'04, following Haase, '89, compares them to the coxal organs of Myriopoda.

The theory of Walton, '00, who considers the "meron" as a vestigial leg, seems likewise highly improbable. From an examination of a large number of insects, it would appear that the meron is merely a portion of the coxa. In such generalized forms as the Blattidæ, it is not at all, or only partially, distinguishable from the remainder of the coxa; but in less generalized forms, as for example the Lepidoptera, it becomes more separated from the coxa, and in the highly specialized, swiftly-flying Diptera it is drawn quite into the pleural region, doubtless as the result of muscular tension.

Walton's other theory, that the pterygoda represent a pair of epimeral wings, is fully as improbable as his meron hypothesis. The pterygoda bear absolutely no resemblance to wings in structure or in development, and, furthermore, no fossil remains show any traces of more than one pair of wings to each thoracic segment. Walton has tried to evade these facts by suggesting that the tegulæ, etc., are wing "fundaments." With regard to this supposition, all that can be said is, that, so far as our present knowledge extends, the tegulæ have fundamentally nothing in common with wings, and any attempt to discuss what they might develop into belongs wholly to the realm of speculation.

If, as Patten, '90, states, two pairs of tracheal invaginations occur in each segment of *Acilius*, this would indeed be a strong proof of segmental fusion. In the adult *Acilius*, however, this is certainly not the case. Embryos of this insect were not accessible, but in the embryos of *Chrysopa*, and the far more primitive *Forficula*, there are no traces of more than one tracheal invagination to the segment. Furthermore, in all illustrations of other insect embryos that I could find, only one tracheal invagination is indicated in each segment, and there are no evidences of a double nature in the ganglia or any other important segmental structures.

This lack of embryological evidence is the chief argument against the hypothesis of segmental fusion, and until proof more convincing than that brought forward in support of the above cited theories can be offered, it would seem preferable to adopt a mechanical explanation —as, for example, muscular tension, etc.—to account for the origin of the separate sclerites.

In attempting to apply this thery it must be borne in mind that the sclerites are not produced in a more or less haphazard fashion, as such extremists as Graber seem to think, but one can trace the systematic following out of a ground plan common to all three of the thoracic segments.

Lowne, '90, is quite incorrect in his statement that the prothoracic sclerites cannot be homologized with those of the other two segments, as a glance at the thorax of any Blattid would have convinced him. His criticism of Audouin, '20, for taking as a type so "specialized" a segment as the wing-bearing one, is likewise wholly unjustified; for a comparative study can lead to no other conclusion than that the segment bearing the functional wing has undergone the least modification. The prothorax in many cases has been reduced to a mere collar, and, indeed, Brongniart, '90, finds that in certain fossil insects this segment bore a wing-like appendage which has since been lost. The prothorax, then, cannot be chosen as a type, and in the segment which does not bear the functional wing—as for example the metathorax of the diptera—it is convincingly apparent that there has been a great fusion and reduction of both sclerites and muscles. It is the wing-bearing segment, therefore, that more nearly represents the primitive condition, and if Lowne had not confined his attention to a specialized species of the highly specialized dipteran order, he would have seen how illogical are his conclusions for insects in general, based upon so modified a form.

General Description.

The Tergum.—As has been previously stated, the structure of the prothorax is essentially the same as that of the other two segments. This principle, however, may lead to a mistaken interpretation of the condition exhibited in the prothoracic tergum (or the pronotum, as Burmeister, '32, terms it) of certain insects. Thus most text-books state that in the grasshopper's pronotum, the ring-like areas, produced by a series of transverse furrows, represent the præscutum, scutum, scutellum and postscutellum—as is figured by Brooks, '82, for example. Theoretically this sounds very plausible, but a comparison with a large number of Saltatoria shows that these wrinklings are largely of a secondary nature. Not only is the musculature quite different, but it is likewise the case that the four subdivisions of the meso- and metathoracic terga never occur as such regular, parallel rings. In addition to this, in certain Acrididæ (*Dictyophorus* for example) there are even more than four rings, and in some cases the transverse furrows which mark off these rings are interrupted, thus showing their secondary character.

The præscutum and postscutellum usually form what Kirby, '28, terms a phragma—that is to say an inward projecting process of the tergum. Such a præscutum or postscutellum has never been described

for the prothorax, and it would appear that if such structures ever existed in the pronotum they have since been lost through reduction or fusion with the scutum and scutellum.

The Præscutum.—As has been stated, it is impossible to distinguish a præscutum in the prothorax, but in the mesothorax this sclerite is frequently represented by a well developed phragma (fig. 1, N_1). This phragma is apparently a portion of the tergum drawn inward and downward by muscular tension, and is separated from the scutum by the line of attachment of the intersegmental membrane, beneath which the phragma projects into the body cavity.

In his earlier works Audouin did not distinguish between the phragma and the triangular portion of the scutum immediately behind it (N_{2a}), terming both together the præscutum. In this usage he has been followed by Packard, '98; but most authors use the word præscutum as synonymous with Kleuker's protophragma—in other words the præscutum is only the anterior phragma of the tergal region.
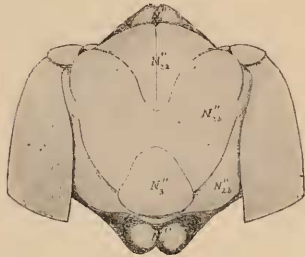

Fig. 1.—MACROXYELA.—Dorsal view of the mesothorax, showing the subdivisions of the tergum or notum. For reference letters, see list at end of the paper.

The præscutum of the metathorax is frequently fused with the postscutellum of the preceding segment or it may be greatly reduced. On this account Kleuker, '83, terms the second phragma the deuterophragma, whether it is composed of the mesothoracic postscutellum, the metathoracic præscutum, or of both together. It would seem preferable, however, to use Audouin's terminology, which is not only more exact, but also has the right of priority.

On either side of the mesothoracic præscutum of such insects as *Myrmeleon, Mantispa*, etc., are two bridge-like plates lying just in front of the wings, and connecting the tergum with the upper portion of the episternum. These plates appear to represent the so-called præsegmental lamellæ described by Voss, '04, in the thorax of *Gryllus*. Since these plates are not internal lamellæ, in most insects, but occur usually as external sclerites, they will be here referred to as the præsegmental sclerites.

The Scutum.—The thorax of *Dytiscus*, which Audouin, '24, chose as his type for insects in general, is too greatly modified to show the normal relations of the tergal subdivisions, but fortunately Audouin, '32, has given a more serviceable description in his translation of MacLeay's

article on *Polistes*.   By comparing the thorax of *Polistes* with that of certain other less specialized Hymenoptera, such for example as *Macroxyela, Tenthredo*, etc., in which the mesonotum has retained a comparatively primitive condition, it is an easy matter to apply Audouin's terminology to insects in general.

In the mesothorax of *Macroxyela, Chrysopa, Myrmeleon*, etc., the portion of the tergum just behind the præscutum is composed of two regions: a median portion triangular in shape, with its apex directed caudad (fig. 1, N_{2a}), and a larger portion surrounding the first laterally and posteriorly (N_{2b}).   The triangular median region of the scutum may be termed the mediscutum, and the remainder the parapsidoscutum (from MacLeay's, '30, parapsides, applied to two pieces separated off from this region in *Polistes*).

In his description of *Dytiscus*, Audouin regards the mediscutum as part of the præscutum, while in his translation of MacLeay's work he speaks of the region corresponding to the mediscutum as the scutum proper, and likewise reckons the parapsides to the scutellar region. The latter division is the only natural one, and has consequently been adopted in this discussion.

In the Hymenoptera, one can trace an extremely interesting series of changes in the scutellar region of the mesothorax.   Thus, if one examine the thorax of *Macroxyela, Abia, Odynerus* and *Chrysis*, in the order given, it will be seen that the apex of the triangular mediscutum (figs. 1 and 2, N_{2a}) becomes gradually lengthened out, and pushes through that portion of the parapsidoscutum (N_{2b}) behind it until it reaches the scutellum (N_3).   Its sides then begin to open out, and become nearly parallel.   By this process the formerly triangular mediscutum assumes a rectangular form (fig. 2, N_{2a}), and divides the parapsidoscutum into two widely separated halves (N_{2b} and N_{2b}), the parapsides of MacLeay, '30.

As shown by MacGillivray, '06, the wing veins of the Xyelidæ show that this family is the most generalized of the Hymenoptera.   Consequently the thorax of *Macroxyela* is more primitive than that of *Polistes*—an opinion which is confirmed by a comparison with certain lower insects, such as *Myrmeleon*,
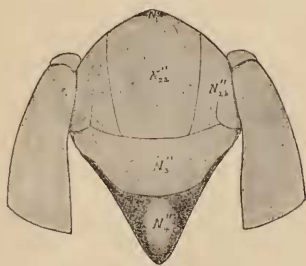

Fig. 2.—E u m e n e s.— Dorsal view of the mesothorax. A comparison with fig. 1 shows that the mediscutum (N''_{2a}) has pushed through the parapsidoscutum (N''_{2b}) and divided it into the two "parapsides" (N''_{2b} and N''_{2b}).

etc.   If this be true, one is justified in assuming that the "parapsides'

of *Polistes* are but portions of the mesothoracic parapsidoscutum. MacLeay's suggestion, that the mesothoracic parapsides are but the prothoracic paraptera(!) pushed back from their original position, must, therefore, be regarded as entirely untenable.

The parapsidoscutum is very closely connected with the organs of flight; and indeed its caudal portion appears to merge into the membranous anal region of the wing.

Along the sides of the scutum lie a number of small plates which are usually free, but may be more or less fused with one another or with the scutum. Jurine, '20, has described six of these for Hymenoptera, but only three are of particular importance. The first of these is found at the base of the costal region of the wing, and has been termed the antesigmoid by Amans, '85; the second, which Amans terms the "piece quadrilatere" (sigmoid), is situated at the base of the median region of the wing; and the third or dorso-terminal lies at the base of the anal region of the wing. The structure and mechanism of these sclerites has been described in detail by Amans, '85, and Voss, '04, and need not, therefore, be further discussed here.

In addition to the above-mentioned sclerites, there occur two plates (one at the base of each wing) which have been variously termed squæmula, tegula, paraptera, pterygoda, etc. Of these terms, Latreille's, '20, "pterygodes" or pterygoda appears to have the right of priority, and on this account has been here adopted. In *Gryllus*, Voss, '04, has described a structure which he terms a "Hautpolster," but does not compare it with other insects. This structure is beyond a doubt homologous with the pterygoda, and bears the characteristic hairs. In the Trichoptera, although still somewhat "Polster"-like, it is more strongly chitinized, and in the Hymenoptera it forms a horny scale, covering the base of the wing. In certain Lepidoptera the pterygoda are greatly developed and are densely beset with hairs. Westwood, '39, has confused these with the patagia of the Lepidoptera, but they are doubtless quite different structures.

The Scutellum.—Behind the scutal region lies a small, medianly-situated scutellum (fig. 1, N_3). In form it may be somewhat semicircular, oval, shield- or wedge-shaped. In the latter case its anterior end is embedded in the parapsidoscutum. Its posterior margin is usually drawn out into a narrow strip on either side, and is continued in the posterior margin of the anal region of the wing.. This character is frequently very useful in determining the boundaries between the mesoscutellum and phragma, or to distinguish the mesoscutellum from the metanotum when these are partially fused.

Voss, '04, appears to consider the scutellum as part of the scutal region, and terms it the "unpaares mittelfeld." This terminology, however, would be incorrect for three reasons: in the first place, because the sclerite in question does not belong to the region which Audouin, '24, calls the scutum, but is what he terms the scutellum; furthermore, the unpaired median region of the scutum, if such existed, would be the triangular mediscutum; and, lastly, there is no "unpaired" region, strictly speaking, in either scutum or scutellum, as the whole tergum was originally divided into two symmetrical halves by a median longitudinal suture.

This suture, according to Comstock, '02, represents the line of closure of the embryo, and it is along this line that the cuticle is ruptured at the time of moulting. The median dorsal suture may be spoken of as the mid-dorsal suture, while the corresponding median ventral suture (which may represent traces of the neural groove) will be referred to as the mid-ventral suture.

The mid-dorsal suture is easily seen in such insects as the Sialidæ, Perlidæ, Tenthredinidæ, Psocidæ, Tipulidæ, Trichoptera, etc. In certain other insects, and some of these are very primitive, as, for example, the roaches and earwigs, one can find scarcely any traces of this suture in the mesothorax, since the tergal subregions have united to form a simple undivided notum. However in the metathorax of some Blattidæ, etc., one can distinguish faint traces of these parts. This leads to the conclusion that the simple notum is the result of non-usage of the wings, or the peculiar mode of life of these insects, and would hence be a tertiary modification rather than a retention of the primitive condition.[1]

An examination of the inner ridges, which serve as points of insertion for certain muscles, suggests that the tergum at one time may have been a single piece, but, though muscular tension, ridges were drawn inward, thus creating corresponding furrows or sutures on the exterior surface. It is possible that the so-called parapsidal furrows, or sutures separating the medi- from the parapsido-scutum, were formed in this way, as is likewise the case with the furrow which separates the parapsidoscutum from the scutellum. The latter furrow may be spoken of as the scutellar suture.

The Postscutellum.—Behind the scutellum lies the postscutellum (fig. 1, N_4), which usually occurs as a phragma projecting more or less into

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[1] In the Apterygota, however, the simple, undivided notum doubtless represents the primitive condition.

the body cavity, or, as is the case in the Diptera, it may be largely external (see figs. 7 and 8, N_4).

The postscutellar phragma is usually much larger than the præscutal phragma, and, while the latter is always closely connected with the scutum, the postscutellum may become almost completely separated from the remainder of the tergum.

As has been stated, the præscutum and postscutellum usually occur as phragmas, and between them extend the dorsal longitudinal muscles. It would appear that the arching of the mesothoracic region in such swift-flying insects as the Hymenoptera, Diptera, etc., is caused by the tension of these muscles. In the Diptera, the mesothoracic postscutellum is greatly developed to furnish an attachment for these powerful muscles, and the whole mesothorax appears to have grown at the expense of the metathorax, which shrinks away, as it were, thus exposing the huge mesothoracic postscutellum. Muscular tension is doubtless another factor causing the mesothoracic postscutellum to become external, since it would give rise to an arching upward of the tergum and the shifting forward of certain of the sclerites, as will be later discussed. This external character and unusual development of the mesothoracic postscutellum in the Diptera caused Latreille, '20, to mistake it for the notum of the metathorax. He consequently homologized the metathorax of the Diptera with the first abdominal segment (the "segment mediaire") of the Hymenoptera. MacLeay, '30, committed a somewhat similar error in considering the first abdominal segment (which is closely connected with the thorax in pedunculate Hymenoptera) as part of the metanotum. Consequently, that portion which he terms the postscutellum in *Polistes* belongs to the abdominal region.

The postscutellum[2] (fig. 7, N_4) of the Tipulidæ is greatly developed and is distinctly divided into three regions—a median region which may be termed the mediophragmite (N_{4a}), and two lateral regions which will be spoken of as the pleurophragmites (N_{4b}). Each of the pleurophragmites may be subdivided into a superior (N_{4bs}) and inferior (N_{4bi}) region, and the mediophragmite likewise may be divided into symmetrical halves by a continuation of the mid-ventral suture.

In certain insects in which the pleurophragmite is not connected with the pleura, it would appear that a portion of the pleurophragmite

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[2] Snodgrass, '08, frequently states that the Orthoptera have no postscutellum. This is not the case in the Gryllidae, for example, as the postscutellum of *Gryllus domesticus* is quite well developed.

becomes separated off and remains connected with the epimeron. This piece has been termed by Kolbe, '93, the "parapleure" in the Coleoptera, but this term is quite differently applied by other investigators. Thus Voss, '04, considers "parapleura" as synonymous with episternum. On the other hand Cuvier, '23, states that the "parapleuræ" are the "epimeres." According to MacLeay, '30, the "parapleuræ" are the episterna. Latreille, '20, considers the parapleuræ as the "epimeres du metathorax." Lacordaire, '54, speaks of the epimeron and episternum together as the "parapleures," and erroneously ascribes this usage to Audouin. According to Knoch, 1801 (who introduced the term), "parapleururum" would refer to the episternum; while the episternum and epimeron together were termed "parapleururum duplum." If we are to abide strictly by the rule of priority, the term parapleuron would apply only to the episternum, in which sense it is used by Knoch, 1801, Kirby, '28, MacLeay, '30, Burmeister, '32, Fieber, '61, Voss, '04, and others. However, in the sense used by Kolbe, '93, it is a very useful term, if so used that there would be no danger of confusion with the above cited usages.

Amans, '85, gives a terminology for the tergal subdivisions entirely different from that here accepted. Thus he proposes the names prodorsum, dorsum, postdorsum and sub-postdorsum for exactly the same sclerites which Audouin, '24, had previously termed the præscutum, scutum, scutellum and postscutellum. Enderlein, '03, has recently adopted Amans' usage, but there appears to be no just cause for thus arbitrarily changing Audouin's terminology, which not only has the right of priority, but also has the advantage of widespread acceptance, and is not open to the objection mentioned by Audouin himself, namely, the term dorsum should be applied only to the entire dorsal surface of the insect, in contradistinction to the venter, ventrum or ventral surface.

As has been previously mentioned, Kleuker's, '83, terminology is inexact, in that he does not distinguish between the postscutellum of the mesothorax and præscutum of the metathorax, but terms them indiscriminately the deuterophragma. Moreover, Voss', '04, substitution of the term postscutum for postscutellum is quite unwarranted, and it would appear far preferable to employ only the simple and appropriate terminology of Audouin, '24.

THE WING.—The wing, as we have seen, is very closely connected with the parapsidoscutum, and indeed Packard, '98, believes that the wing fundaments are scutal structures. They usually arise as sack-like folds of the body wall, and in insects with incomplete metamorphosis

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appear as lateral outgrowths of the caudal margin of the tergum. This is well shown in the development of the male Blattid, in which the elytron-like fore wings project from the posterior margin of the tergum, becoming more and more elongate at each moult, and finally develop into chitinous structures in which the characteristic venation of the wings is clearly shown. This has led to the theory that the wings arose as lateral outgrowths of the margin of the notum, originally acting as a sort of parachute, but later developing into functional wings. Another theory is that the wings and legs have a similar origin. In a third theory, it is claimed that the wings develop from tracheal gills; and in yet another, it is held that the wings are modified spiracles. It is not proposed to discuss these theories here at length, but, in objection to Gegenbauer's, '78, tracheal-gill theory, it may be remarked that Palmen, '77, has clearly demonstrated that the closed tracheal system is only a secondary adaptation to the aquatic life of the larva, and that aerial respiration was doubtless the primitive one. On this account, it is hardly probable that wings have developed from tracheal gills.

Walton, '01, believes that the tegulæ or pterygoda are rudimentary wings, but, as has been previously discussed, there is absolutely no proof for the statement that these structures are wing fundaments, either from an embryological or a structural point of view. Comstock, '95, suggested that "the wing covers or elytra of earwigs and beetles probably correspond to the tegulæ . . . . . that is, they are a pair of side pieces of the mesothorax, the parapleura, greatly enlarged." Walton has followed out this suggestion in his theory, and likewise adopts the view that the alulet-like structures under the elytra of *Hydrophilus*, etc., represent extra wings. Comstock, '98, however, has shown that the elytra are the modified wings, and that the membranous structures beneath them are quite comparable to the alulæ of Diptera, etc., and are even bordered by the "spring vein" characteristic of the alulæ.[3]

In the most generalized insects the tracheation follows the path indicated by the chief cuticular thickenings, which later become the veins for stiffening the wings. The tracheation, therefore, is frequently of great value in determining the homology of the principal wing veins, and was much used by Comstock, '98, in the comparison of the venation throughout the orders. The principal veins recognized by him are the costa, subcosta, radius, media, cubitus, and the anals.

[3] See Sharp, '96.

This terminology, based upon that of Redtenbacher, '86, is the one usually accepted by modern systematists, and has consequently been here adopted.

THE PLEURON.—The two principal sclerites of the pleuron are the episternum and epimeron of Audouin, '24. The later terms, antepleuron (episternum) and postpleuron (epimeron) of Amans, '85, or the coxopleure (episternum) and anopleure (epimeron) of Verhoeff, '03, since they are applied to exactly the same sclerites, must be regarded as superfluous synonyms. The pleurit and subcoxa of Heymons, '99, will be later discussed under the heading Hemiptera. However, it may be remarked of these sclerites—which have given rise to a great deal of discussion—that the pleurit is merely the epimeron, while the greater part of the subcoxa corresponds to the episternum.

The pleurites of the Blattidæ are interesting from the fact that the epimeron and episternum appear to be merely portions of a single plate separated into two regions by a deep pocket-like infolding of the integument. This suggests that the episternum and epimeron may originally have been one piece, but became separated by such an infolding of the integument—possibly due to muscular tension. In this way there would be formed an external furrow, the so-called pleural suture, and a corresponding hollow ridge, the entopleuron or apodeme. This would account for the fact that the apodemes of insects are hollow processes, and it is conceivable that the apodemes would thus arise as hollow invaginations of the body wall of the embryo, even though the muscular tension which originally developed the apodemes were not strongly operative at this stage.

There is a great lack of uniformity in the usage of the terms apodeme and apophysis in referring to the internal or "entothoracic" processes. As here used, the expression apodeme is applied solely to internal processes of the pleuron (i.e., the "entopleura"); while the term apophysis refers only to the internal processes of the sternum—the "entosterna."

The entopleuron may bear four inward projecting processes as follows: above, a pivot, or articulating process for the wing, which may be termed the alar process of the apodeme; and below this a process serving for muscle attachment (in such insects as Panorpa, etc.), which may be termed the intermedian process. The third is usually quite a large process. It may or may not extend as far as the furca (or forked apophysis of the sternum), but frequently abuts against the end of the furcal arm, and may even fuse with it. This process will be referred to as the adfurcal process. The process just below it, which

forms an articulation with the coxa, has been termed the coxal process. These processes will be discussed more at length in a later article dealing with the comparative myology of insects.

The Epimeron.—It is generally taken for granted that the epimeral and episternal regions of the thorax are not subdivided into smaller sclerites, but a glance at the mesothorax of *Cicada* (fig. 5) and *Tipula* (fig. 7) or the metathorax of *Myrmeleon* (fig. 4) and *Chrysopa* (fig. 3) will readily convince one that this is an error.

To illustrate, let us examine the thorax of the widespread insect *Chrysopa*. For this purpose *Chrysopa vulgaris* is preferable to the somewhat commoner form *Chrysopa perla*, as the black bars and markings upon the thorax of the latter insect tend to obscure the sutures between the subregions.

In the epimeral region of *Phassus* (fig. 6), and most winged insects as well, one can readily find an elongate plate embedded in the softer cuticule directly under the posterior portion of the wing (EM_c). This sclerite doubtless corresponds to the plate which Lowne, '90, designates as the "costa" in the blow-fly. The term costa, however, has been applied to one of the wing veins, and this usage has been everywhere adopted. It would, therefore, seem preferable to substitute the expression costal sclerite in referring to the above mentioned plate.[4] The costal sclerite bears an internal process, which serves as
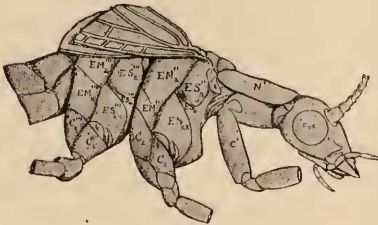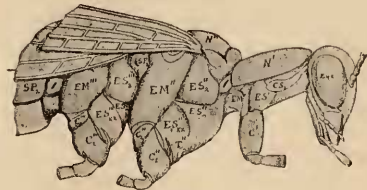

Fig. 3.

Fig. 4.

Fig. 3.—CHRYSOPA.—Lateral view of right flank. Abdomen, legs, wings and antennæ partially removed.
Fig. 4.—MYRMELEON.—Side view of right flank. Abdomen, legs, wings and antennæ partially removed.

the point of insertion for the epimeral wing muscles. This process may be termed the endocostal process. Behind the costal sclerites there frequently occurs a smaller sclerite which likewise serves as an attachment for the epimeral muscles. This will be spoken of as the

[4] Snodgrass, '08, terms this sclerite the "postepimeron," but since the plate in question is normally "supraepimeral" rather than "postepimeral," Lowne's term, slightly modified, has been here retained.

posterior costal sclerite (EM_{2c}).   It is usually very small and relatively unimportant.

In the metathorax of *Chrysopa* and *Myrmeleon*, and in the mesothorax of Cicada, etc., the epimeron is distinctly divided into an upper and lower portion.   The upper region will be referred to as the anaepimeron[5] or anepimeron (fig. 3, EM_a) and the lower region may be termed the kataepimeron or katepimeron (EM_k).   In the Raphidians, the suture between the anepimeron and katepimeron is partly obliterated, and in many other insects all traces of it have disappeared.   In *Phassus schamyl* (fig. 6), the upper portion of the epimeron is membranous, thus suggesting that in other insects the anepimeral region may have originally arisen as a softening of the chitin, to give greater freedom of motion to the wing, and thus become differentiated from the remainder of the epimeron.

In the Muscinæ, there is an arching of the mesothorax and a shifting forward of the sclerites—probably the result of muscular tension—so that the upper region of the epimeron (EM_a) is bent forward and lies upon the episternum (fig. 8).   It would appear that Lowne, '90, and other dipterologists have not been aware of this fact, for Lowne, Hewitt, '07, and a number of others mistake the anepimeron (EM_a) for the episternum and consequently designate the katepimeron (EM_k) as the entire epimeron.

Fig. 5.—CICADA.—Lateral view of right flank.   Abdomen, legs, and wings shortened.

A comparison with one of the Tipulidæ—in which group the sclerites are in their normal positions—readily shows the error of such a homologization.   In the Tipulidæ, and less distinctly in the Ephemeridæ, the pleurophragmite (or lateral region of the postscutellar phragma) is so closely connected with the pleuron that it appears to be a part of the pleural region (fig. 7, N_{4bs}); but, with the "parapleure" of the Coleoptera, it should be classed as a portion of the postscutellum.

Connected with the lower portion of the epimeron in *Chrysopa* and a number of other insects is a sclerite termed the meron (fig. 3, C_2).
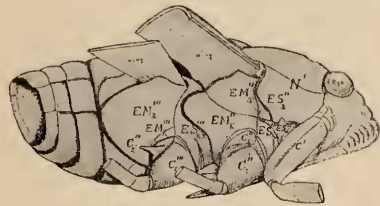
[5] In an earlier publication (Crampton, '08) the term hyper- and hypo-epimeron were employed to designate these regions, but, upon further consideration, it has seemed preferable to substitute the designations ana- and kata-epimeron, which are not so confusingly similar as the former terms.

This sclerite is of a variable nature, being entirely coxal in some insects, while in others it is entirely pleural. The origin and nature of this sclerite will be more fully described in the discussion of the sclerites of the leg.

The Episternum.—While the division into ana- and kata-epimeron is shown in but few hexapods, a subdivision of the episternum into an upper and lower region is evident in a great number of insects. Among these may be mentioned *Sialis, Hepialus, Corydalis, Phassus, Bittacus, Cicada, Tipula, Mantispa, Hemerobius, Raphidia, Chrysopa, Myrmeleon,* the Nemoptera, Trichoptera, and a large number of other insects from different families. Beyond a doubt, if enough material could be examined, it would be found that indications of this division occur in some genera of every family.
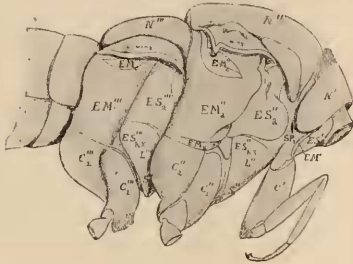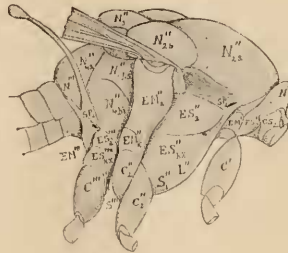

Fig. 6.

Fig. 7.

Fig. 6.—PHASSUS.—Lateral view of right flank. Head completely removed; wings, abdomen and two posterior legs shortened.
Fig. 7.—TIPULA.—Lateral view. Head entirely removed. Wings, abdomen and legs shortened.

The epimeral subdivisions are best shown in *Mantispa*, but *Chrysopa* serves the purpose almost as well, and is a much commoner insect. In *Chrysopa*, the upper region of the episternum—which will be termed the anepisternum (fig. 3, ES_a), is separated from the lower or "katepisternum" (ES_k), by a narrow strip which may be spoken of as the median region of the episternum (ES_m). In the thorax of *Chrysopa* this strip is very narrow, but in the thorax of *Myrmeleon* it is quite broad (fig. 4, ES_m). In the metathorax of the Forficulidæ, the upper portion of the anepisternal region is frequently cut off by a white, scar-like softening of the chitin of the episternum. Verhoeff, '03, terms this piece the pteropleure.[6]

While the anepisternum in most insects is in its normal position, the

[6] The musculature of the anepisternum clearly shows that it is not to be homologized with the "pteropleure" alone.

previously mentioned shifting forward of the anepimeral region in the Muscidæ (fig. 8, EM_a) has displaced the anepisternum (ES_a) in the mesothorax. This phenomenon has led to a great variety of interpretations of these sclerites in the Diptera. Thus Brauer, '82, refers to the anepisternum (fig. 7, ES_a) as the entire episternum, and the katepisternal region (ES_k) as the sternum. Lowne, '90, mistakes the anepimeron (fig. 8, EM_a) for the entire episternum, and, therefore, terms the anepisternum (ES_a) the "lateral plate." Hammond, '81, commits the same error and terms the anepisternum the parapteron. The latter term, however, cannot be used in this connection, as Audouin, '32, made it synonymous with squamula, i.e., the tegula or pterygodum. As first employed by Audouin, '24, the designation parapteron was applied to the anterior margin of the episternum. Audouin himself seems to have had a great deal of trouble in homologizing this region with that of other insects, and finally solved the difficulty by applying the terms hypopteron and parapteron to MacLeay's, '32, squamula— with which they are therefore synonyms, and are so used by most authors.

On the inner surface of the anepisternum of *Chrysopa*, *Corydalis*, and a number of other insects, one can distinguish a lobe-like struc-
ture which is apparently formed by the inrolling of the anterior margin of the anepimeron, and serves as an attachment for the muscles extending to the trochantin and leg. It is quite easy to follow the modification of this structure in various insects, as it gradually becomes more separated from the anepisternum, assumes a conical form, and is finally connected with the upper portion of the episternum by its apex alone. This plate will be spoken of as the conus.

Fig. 8.—MUSCA.—Lateral view. Head entirely removed; wings, abdomen and legs shortened. A comparison with fig. 7 shows that in the Muscinæ there is a shifting forward of the parts, as is indicated by the arrow.

The Laterale.—If one compare the mesothorax of a Blattid with that of a Forficulid, it will be seen that the so-called episternum is not the same in both. In order to better understand the relation of the sclerites in these insects a hypothetical type (fig. 20) has been taken as a basis for comparison. In the stage here represented, the epimeron (EM) is indicated as a distinct region, while the remainder of the pleuron
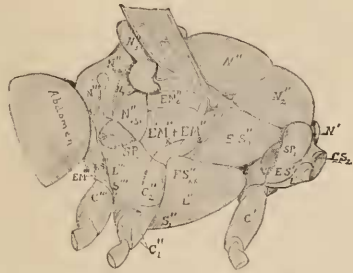
($ES' + L$) consists of a single piece which may be designated by Heymon's, '99, term subcoxa.[7] However, it should not be taken for granted that in adopting Heymon's terminology, his theory of the origin of the subcoxa is likewise accepted; for, as will be later discussed, it is very improbable that the subcoxa is the basal portion of the leg.
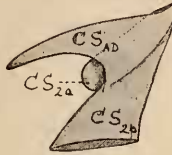

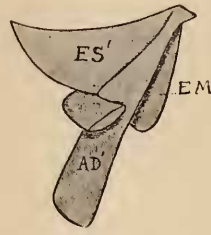
Fig. 9.   Fig. 10.   Fig. 11.

Fig. 9.—DOLERUS.—External view of the right cervico-pleuron (*i.e.*, union of the cervicals with the prothoracic pleuron). This region is usually termed the prothoracic episternum.

Fig. 10 represents the anterior portion of fig. 9, seen from within to show the apodeme-like structure (CS_{ad}) separating the anterior lateral cervical (CS_{2a}) from the posterior lateral cervical (CS_{2p}).

Fig. 11 represents the posterior portion of fig. 9 seen from within; showing the apodeme (AD') between the prothoracic episternum (ES') and epimeron (EM').

The trochantin (T) is represented as a portion of the subcoxa, though it is quite possible that it was originally a portion of the coxa, separated off by muscular tension, and united with the subcoxa as a secondary modification. For the present, however, this point may be left out of consideration.

The first division of the subcoxa doubtless occurred along the line $a\ c$ (fig. 20), thus separating the subcoxa into the episternum (ES) and a region which may be termed the laterale (L). The further divisions in the laterale may occur in either of two directions—longitudinally or transversely. A longitudinal division (*i.e.*, along the line $c\ i\ g$) would produce the condition found in the cockroach (fig. 21, compare also pl. III): that is, there would be a separation into an anterior region, which may be termed the anterior laterale[8] (L_a), and a posterior one, which may be termed the antecoxal laterale (L_b). The latter term is a slight modification of Walton's, '00, "antecoxal piece," which has priority over Verhoeff's, '03, "katopleure." If, on the other hand, the laterale be divided, not longitudinally (as in the

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[7] According to Enderlein, the "subcoxa" represents the trochantin; Börner considers it the equivalent of his merosternum; and Verhoeff homologizes it with his coxopleure and trochantin.

[8] In a former publication this sclerite was termed the "pleuro-laterale."

cockroach), but transversely, *i.e.*, along the line *f e* (fig. 20), we would have the condition found in the earwig (see fig. 19, compare also pl. II). The region nearest the episternum (ES) may be termed the episternal laterale (L_1), and that next the sternum (S) the sternal laterale (L_2). In *Forficula* there is a third piece, the "hyposternal laterale" (L_3), which is not so deeply pigmented as the other two. It is usually covered by the sternum, and in *Anisolabis* it appears to be fused with the sternal laterale.

The interpretation of the relations of these sclerites as given by Verhoeff, '03, differs very widely from the one just discussed. This investigator homologizes the episternum of the earwig (fig. 19, ES) with the episternum plus the anterior laterale in the cockroach (fig. 21, $ES + L_a$). The earwig's episternal laterale (fig. 19, L_1) he homologizes with the antecoxal laterale of the cockroach (fig. 21, L_b); and as the earwig's sternal laterale (fig. 19, L_2) would then have no corresponding sclerite in the cockroach, Verhoeff seeks to explain the sternal laterale as a "Vorplatte" or anterior plate which lies in front of the sternum in the prothorax (*i.e.*, a lateral cervical?), but in the meso- and metathorax it is supposed in some way to become drawn around to the side of the sternum and take up a position between the latter and the antecoxal laterale (or "katopleure"). The musculature gives no indication of such a caudad migration of the lateral cervicals, or of any other "Vorderstück," and it is difficult to see how such a theory can be supported. On the other hand, it is quite comprehensible that a transverse, as well as a longitudinal division might occur, since a similar division is clearly traceable in the prothoracic trochantin of the Blattidæ.

In the metathorax of the Dermaptera (or Euplexoptera) the sternal laterale has apparently fused with the sternum (pl. II). In the prothorax of *Anisolabis* (pl. II) the episternal laterale (L_1) has partially fused with the episternum, but traces of its outlines are still preserved. The sternal laterale may be readily observed as a distinct sclerite (L_2), but both it and the episternal laterale (L_1) are greatly reduced in size. The prothoracic sternal laterale (L_2) is entirely distinct from the cervical sclerites (CS_{2x}), which lie in a plane below it;
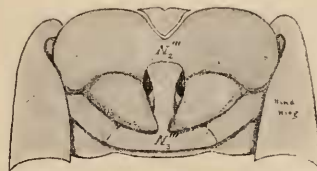

Fig. 12.—PTEROSTICHUS.—Dorsal view of the metathorax, showing the sternellum (N'''_s) partially covered by two flaps of the parapsidoscutum.

yet Börner, '03, confuses it with the cervicals, and homologizes it

(the prothoracic sternal laterale) and one of the cervicals with the mesothoracic episternal laterale of the same specimen.   The remaining sclerites of the posterior lateral cervicals (CS_{2x}) he homologizes with the sternal laterale of the mesothorax.   Börner likewise considers that the mesothoracic sternal laterale (pl. II, L''_2) and episternal laterale (L''_1) are subdivisions of the antecoxal laterale (pl. III, L_b).   These views however seem quite untenable.

The longitudinal division of the laterale into the anterior and antecoxal regions is best shown in the cockroach (pl. III), although it is clearly traceable in a number of insects.   In many Neuroptera, as for example *Corydalis* (fig. 17), *Chrysopa* (fig. 3), etc., the antecoxal laterale appears as a narrow strip (L_b) connecting the katepimeral complex[9] (Es_{kx}) with that portion of the sternum which will be later spoken of as the furci-sternum (S_3).   The anterior laterale (L_a) is usually quite large, filling the region between the episternum and the "Basi-sternum" (S_2).

In the thorax of *Gryllus*, Voss, '04, has described a sclerite which seems to correspond in part to the laterale.   He terms this sclerite the coxosternum, upon the ground that it represents the region so designated by Börner, '03.   This homologizing, however, is quite incorrect, for, as may be readily seen in his figures, Börner's "coxosternum" includes the epimeron, episternum and laterale.   Furthermore, Verhoeff had long before employed the term "coxasternum" to designate the fusion product of the coxæ with the sternum.   The laterale, therefore, can hardly be termed the "coxosternum."

The Trochantin.—The small, somewhat triangular-shaped sclerite articulating with the coxa is designated as the trochantin, trochantine or trochantinus.   In the Blattidæ (fig. 21 and pl. III) the trochantin (T) is quite large, and in some species it is united for a short distance with the episternum.   In the Trichoptera (fig. 18) it would appear that the trochantin has fused with the katepisternal complex almost completely, its extreme tip alone remaining free.   The trochantin may thus completely fuse with the katepisternal complex, or, according to certain coleopterologists, it may fuse with the coxa.

In the prothorax of all the Blattidæ that the writer could obtain the trochantin is transversely divided into two regions, the larger of which may be termed the trochantinus major and the smaller one the trochantinus minor.   This condition seems to be a characteristic of the Blattidæ alone, and may prove to be of systematic value.

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[9] *I.e.*, fusion product of the katepimeron, part of the trochantin, and a portion of the antecoxal laterale.

If one compare the mesothoracic trochantin of a Blattid (pl. III) with that of *Chrysopa* (fig. 3) and *Corydalis* (fig. 17), it appears that the so-called trochantin of *Chrysopa* and *Corydalis* correspond only to the "minor" region in the cockroach. The condition in *Corydalis* indicates that the minor region may become constricted off and form what is usually considered the entire trochantin in certain insects, while the major region fuses with the episternum—as it partially does in the prothorax of the Blattidæ.

In the cockroach this breaking of the prothoracic trochantin into two pieces is so evident that it is difficult to see how Sharp, '95, could have so confused these sclerites in his figure of *Blabera gigantea* (*Cambridge Natural History*, Vol. I, p. 222). He has turned the figure upside down, thus making it more difficult to see what he is trying to show, but it is quite plain that the portion he terms the entire trochantin is only the minor region, while his "epimeron(?)" is the major region of the trochantin. The true epimeron is the sclerite he designates as a fold of the pronotum.

Fig. 13.—LYDA.—Ventral view of the cervicals and prothorax.

In the mesothorax of *Forficula* (pl. II) the trochantin is not transversely, but longitudinally divided into separate pieces (T_a and T_b). In the Blattidæ (fig. 21 and pl. III) this division is indicated by a longitudinal suture—the trochantinal suture—which is present not only in the meso- and meta-thoracic trochantin (T'' and T'''), but also in the major and minor portions of the prothoracic trochantin (T'_1 and T'_2), thus clearly indicating that the latter are but parts of a single piece. Of the two regions marked off by the trochantinal suture, the posterior one will be termed the coxal trochantin[10] (pl. III, T_b) and the anterior region will be referred to as the antecoxal trochantin (T_a).

Comstock, '02, terms the antecoxal trochantin (T_a) the antecoxal piece, and refers to the antecoxal laterale (T_b) as the second antecoxal piece. In using the terms antecoxal trochantin and antecoxal laterale an attempt has been here made to retain Comstock's terms, and yet make it clear to what region the parts so designated belong. It must be borne in mind that Comstock's, '02, antecoxal piece (*i.e.*, the antecoxal trochantin) is not the same as Walton's, '00, antecoxal piece (the antecoxal laterale), and neither of these sclerites corresponds to

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[10] With reference to the designation of this sclerite, the term "accessory trochantin plate" (Snodgrass, '08), of which the writer was not aware at the time the above given terminology was proposed, has the right of priority.

the piece termed the "antecoxal piece" in Comstock's, '95, figure of
Enchroma gigantea (page 503). In the latter case, the antecoxal
piece corresponds to that portion of the sternum which will be later
referred to as the furci sternum. The writer was not able to discover
the original use of the expression, but as early as 1861, Leconte, in
his classification of the Coleoptera of North America, states that a
pair of "horny plates" is found embedded in the membrane of the neck,
and terms these the "antecoxal plates." The plates here referred to
are evidently the cervical sclerites.

As has been mentioned, Comstock, '02, designates the antecoxal
trochantin (pl. III, T_a) the antecoxal piece. On the other hand, he
refers to the coxal trochantin as the entire trochan-
tin. The latter usage, however, is quite incorrect,
for the coxal- and antecoxal-trachantin together
form the trochantin, and it is in this sense that
the term will be used in the following discussion.

Fig. 14.—S t r e b-
lognathus (after
Janet).—A com-
parison with fig.
13 shows the way
in which the cer-
vico-propleura
(*C–Pl*) become
approximated on
the ventral sur-
face, and com-
pletely conceal
the prosternum.

Corresponding to the external (trochantinal)
suture, dividing the trochantin into the coxal and
antecoxal regions, is an internal ridge which may
be termed the endotrochantinal lamella, and the
thorn-like process near it may be termed the endo-
trochantinal process.

Synonyms for the term trochantin are Voss',
'04, præcoxal plate, and Strauss-Durkheim's,
'28, rotule. The term præcoxal plate has little
to recommend it, but it would have been much
preferable if entomologists had adopted the term
rotule; for the latter term better expresses the function of this sclerite,
is not borrowed from vertebrate anatomy, and is not so confusingly
similar to the term trochanter, as is the case with Audouin's trochantin.
However, the name trochantin, or the latinized form trochantinus,
given it by MacLeay, '30, is a very useful term and has received too
wide an acceptance to attempt to change it.

Between the trochantin and the coxa lies a very small chitinous
plate, the complementary coxal sclerite,[11] or "complementary plate"
(Börner, '03), which bears an internal process, the complementary
process, to which are attached certain muscles extending to the epi-
sternum. This small sclerite is frequently fused with the coxa, and the
complementary process then appears as a process of the coxal margin.

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[11] The accessory coxal plate of Snodgrass, '08.

THE LEG.—The coxa is very closely connected with the pleuron in certain insects, and indeed Miall and Denny, '86, consider that the pleural sclerites are "two basal leg-joints which have become adherent to the thorax." From his embryological studies, Heymons, '99, also adopts this view in designating the "subcoxa" as the basal portion of the leg. Börner, '03, at first considered the pleural sclerites as plates which have become separated from the sternum, but he later adopted Heymons' view.

The theory that the pleural sclerites are basal leg-joints appears hardly tenable. In those insect larvæ which have long, well-developed legs (as for example *Corydalis*, *Carabus*, etc.) it is necessary that the muscles have some firm support, and it is doubtless the stimulus of the muscular tension which causes the formation of certain sclerites in the soft integument of the larva. This is certainly a far more reasonable supposition than that the epimeron and episternum would be drawn up from a hard chitinized leg region into a soft pleural region, before the latter region were sufficiently resistant to furnish the needed support for the muscles. In the above mentioned insects, the pleural sclerites first appear near the base of the leg, and it is quite possible that these would appear to arise from the basal region of the embryonic leg mass, as it is impossible to say just where the leg begins and the pleuron ends in the embryonic stages. There is such a shifting, flattening, and distorting of the parts in those forms upon which Heymons bases his conclusions, that he was deceived into considering that the mesothoracic subcoxa (fig. 16) represents the epimeron and episternum together, whereas, in reality, it represents the mesothoracic episternum, laterale, and perhaps the trochantin. On the other hand, the "pleurit," which he considers as representing the metathoracic pleurites, does not belong to the metathorax at all, but is merely the *mesothoracic* epimeron (fig. 15, EM''). This mesothoracic epimeron is thrown into a fold by the shifting forward of the region behind it and overlaps the metathoracic epimeron (EM'''), which escaped Heymons' attention altogether. These facts serve to illustrate how easily the embryonic regions may be confused; and when one takes into consideration that even in the larval stages of the above mentioned insects, the pleural sclerites are first formed so near the base of the leg, it is readily comprehensible that Heymons could have been misled into considering the pleurites as basal leg-joints, since in the embryonic stages (upon which he bases his conclusions) there is no sharp distinction between the leg and pleural region.

It is perhaps worth mentioning in this connection that the katepis-

ternal complex, the antecoxal laterale, the furci-sternum (described later), and the katepimeron form a closed ring about the base of the leg, and might consequently be taken for a portion of the leg region; but, for the reasons above stated, this view would be extremely improbable.

Hansen, '93, compares the trochantin to the coxopodite of the Malacostraca, and homologizes the coxa with the basipodite. He likewise adopts the views of Wood-Mason, '79, and Jourdain, '88, who propose that the styli on the meso- and meta-thoracic coxæ represent the exopodite of the crustacean leg. In a recent article Börner has again brought this theory into prominence. Henneguy, '04, who likewise compares the insect leg with that of the Crustacea, differs from the above-mentioned investigators in that he maintains that the stylus corresponds to the epipodite—not to the exopodite. He argues that if the coxa corresponds to the basipodite, the stylus or coxal appendage must correspond to the epipodite or basipodite appendage, and not to the exopodite, which is the appendage of the coxopodite.

The above-mentioned views seem hardly probable, for all indications point to the fact that insects are not descended from aquatic, but from terrestrial ancestors. Palmèn, '77, has demonstrated that the open tracheal system for aerial respiration is the primitive one, and it may be added that in the development of the Ephemerid embryo, the primordia (or fundaments) of the spiracles may be observed even in the germinal streak. The aquatic life of the larvæ, then, must be regarded as a secondary adaptation; and, therefore, one can hardly attempt to homologize the styli of the insect leg with the exopodite or the epipodite of the aquatic Crustacea.

Banks', '93, theory that the styli are vestigial legs has no foundation other than the extremely improbable supposition that each segment is double. In all probability these structures are modified sensory hairs, or they may be comparable to the movable spine-like structures found upon the legs of certain insects. Verhoeff, who adopts Haase's, '89, view regarding the styli, homologizes them with the coxal organs of the Myriopoda.

As has been stated, Walton, '00, believes that the meron is a vestigial leg, but serious doubt is cast upon this theory by the fact that one can trace the formation of the meron as a coxal sclerite, which is either not distinguishable from the rest of the coxa, or at most indistinctly traceable, in the lower forms, but becomes detached by muscular tension in the highly specialized insects. The view that the tension of the muscles attached to it causes the meron to become detached is

strengthened by the fact that it occurs as a distinct sclerite only in the segments which bear functional wings. Thus it seems to be absent in the prothorax of all the insects which the writer has studied, and no traces of it are to be found in the metathorax of the Diptera, although it is well developed in the mesothorax of these insects.

Since the mode of life is the same among insects and myriopods, and as the legs of both are used in the same manner, it is but natural that there should be a very marked convergence in the structure of these organs. This, however, is not sufficient ground for attempting to change the terminology applied to the segments of the insect leg, as Verhoeff, '03-'04, has done. Even if it could be demonstrated that the joints of the insect leg can be homologized with corresponding ones in the myriopods, the terminology for the leg segments of the myriopods should be adapted to that of insects, as the latter has the right of priority and of widespread acceptance.
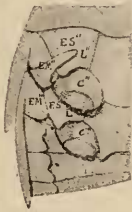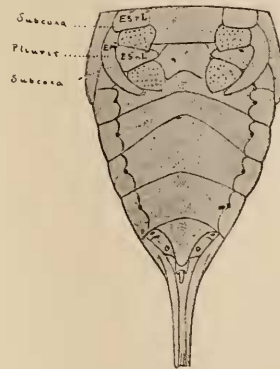

Fig. 15.   Fig. 16.

Fig. 15.—NEPA.—Ventral view showing half of the sternum and the corresponding pleuron of the meso- and meta-thorax and the first three abdominal segments. The flap-like mesothoracic epimeron (EM'') is raised up and bent forward to show the metathoracic epimeron (EM''') which lies under it and was overlooked by Heymons. The corner of the metathoracic epimeron (EM''') is likewise slightly raised to show the first abdominal segment which is hidden by the epimeron, and does not appear in Heymons' figure of Nepa (fig. 16).

Fig. 16.—Heymons' figure of Nepa, slightly modified. The dotted lines indicate the region corresponding to that shown in fig. 15.

Of the leg segments only the coxa and trochanter need be here considered. The coxa is frequently divided into two regions, as has been previously described. Verhoeff's, '03, term eucoxa (fig. 3, C_1), applied to the anterior coxal region, seems preferable to Walton's, '00, "coxa genuina," but for the posterior coxal region Walton's term meron has

been here adopted. A narrow marginal area, the "coximarginal" sclerite, is frequently separated from the rest of the coxa by a suture, as is well shown in the Blattidæ (pl. III, C_m), *Corydalis* (fig. 17), etc. It is questionable whether this region corresponds to the area designated as "C_m (?)" in fig. 18 of the Trichopteran thorax, but the matter is of relatively slight importance.

That portion of the furci-sternum later spoken of as the pedal region (fig. 18, S_3a) frequently occurs as an elongate wedge-shaped process extending into the coxal region. In such cases the furci-sternum is so closely connected with the coxal region that the coxa usually loses much of its freedom of motion. This loss, however, is usually compensated by the greater mobility of the trochanter. Although the trochanter appears to consist of but one joint in many insects, the second joint is frequently hidden within the coxa, so that the "ditrochleate" condition is much commoner than is generally supposed. This fact has led to the formulation of the theory that one of the segments of the trochanter represents a second joint of the "meral" leg. As the author of this theory has not yet published his results, the improbability of such a hypothesis will not be discussed here.

The question as to whether or not the trochanter (or any part of it) is the upper portion of the femur, and the different theories regarding its homology, have but little bearing upon a study of the thoracic sclerites, and need not be further gone into here.

The Sternum.—MacLeay, '30, as has been stated, proposes that each segment is composed of four subsegments or annuli. Arguing from the fact that the tergum is divided into four regions, he states that the sternum likewise "ought to be" divided into four regions, and proposes for these the names præsternum, sternum, sternellum, and poststernellum. He has not figured, described or even seen these regions, but merely assumes their existence because of the condition found in the tergum. Indeed, Newport, '39, who adopts MacLeay's theory, states that these regions cannot all be found in any living insect, as the specialization and fusion of the subsegments have gone too far to leave any traces of the subdivisions in the sternum.

Despite Newport's statement to the contrary, four distinct subdivisions of the sternum are to be found in certain insects, as for example in the thorax of *Nemura* (pl. I). The terminology proposed by MacLeay has not been adopted for the following reasons: the names præsternum, sternum, sternellum, and poststernellum imply a relation between these subdivisions of the sternum and the præscutum, scutum, scutellum and postscutellum, as MacLeay intended

that they should. This relation, however, does not exist, for these subdivisions do not represent four annuli, as assumed by MacLeay. Furthermore, there is this very serious objection to MacLeay's terminology, that the designation sternum cannot be applied to a subdivision of the sternal region, since Audouin employed the name sternum to designate the whole ventral region of the segment, and it is in the latter sense that the term is everywhere used. Lastly, since MacLeay has neither seen, figured nor described these regions, but merely assumes their existence based upon a fallacious hypothesis, his terminology is not binding.

Comstock, '02, although he makes no mention of MacLeay, has attempted to apply MacLeay's terminology to the sternal region. Un-
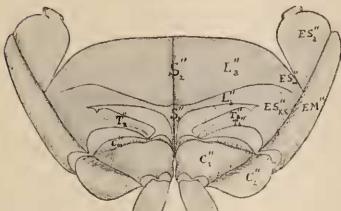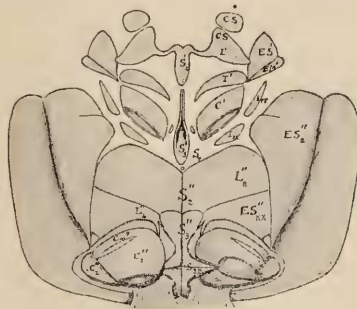

Fig. 17.

Fig. 18.

Fig. 17.—CORYDALIS.—Ventral view of mesothorax. Sternum and pleura spread out in one plane. Legs shortened.

Fig. 18.—HYDROPSYCHE.—Ventral view of pro- and meso-thoracic sterna and pleura, spread out in one plane. Only the basal portions of the coxæ represented.

fortunately both of Comstock's figures (pp. 24 and 25) are of the metathoracic segment, and what he terms the sternellum is the first abdominal sternum. This accounts for the fact that he found no "poststernellum."

The Præsternum.—The name præsternum is the only one of Comstock's and MacLeay's terms here adopted, since only the præsternum in Comstock's figure of *Pteronarcys* (p. 24) has a corresponding region in the sternum of *Nemura* (pl. I, S_1). This term, however, has been adopted without reference to Meinert's, '67, præsternum, mentioned in his description of *Japyx*.

The Japygidæ are such rare insects that the writer was unable to procure a specimen for dissection, and it is therefore impossible to state here, with any degree of certainty, to what extent the præsternum

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and poststernum of Meinert correspond to the regions here designated as the spini- and furci-sternum.   Meinert gives no description of his præ- and post-sternum, other than the brief statement that they are chitinized double folds lying between the segments.   Verhoeff, '04, and Börner, '03, make no attempt to employ Meinert's terms in their figures, but from a study of these illustrations one might hazard the opinion that Meinert's præsternum does not correspond to Comstock's, '02, præsternum at all, but is probably the furci-sternum, later described.

In all probability the præsternum is merely a portion of the large sternite lying behind it, and exists as a separate piece in but few insects. It is usually the first sternite to disappear, and its small size makes it of relatively little importance.

The Basi-sternum.—Just behind the præsternum is a large sternite forming the greater part of the sternal region.   This sclerite, which may be termed the basi-sternum (pl. I, S_2), is frequently fused with the anterior laterale and katepisternal complex to form the "sterno-pleura" of Osten-Sacken, '84.   The basi- and furci-sternum are usually symmetrically divided by a longitudinal furrow—the "mid-ventral" suture.

The Furci-sternum.—Immediately caudad of the basi-sternum is a somewhat smaller sternite, which bears the furca or internal forked process of the sternum.   On this account the sclerite in question has been termed the furci-sternum.   In the swiftly flying insects there is usually an internal "mid-ventral lamella," or ridge corresponding to the mid-ventral suture, and as this is frequently continuous with the shaft of the furca, it may appear as though the base of the furcal shaft arises in the basi-sternum.   This, however, is only a secondary modification, for in the primitive forms the furci-sternum alone bears the paired apophyses.   Externally it is a comparatively easy matter to distinguish between the basi-sternum and the furci-sternum, even when these are not entirely separate sclerites, as traces of the "intrasternal" suture (which separates the basi-sternal from the furci-sternal region) are retained in a great number of insects.

In the Gryllidæ the furci-sternum (which is very closely connected with the basi-sternum) is bent inward, so that its surface forms an angle with that of the basi-sternum.   This bending inward of the furci-sternum causes it to be concealed by the sclerites which follow it and this doubtless accounts for the fact that Voss, '04, did not mention this region in his description of the thorax of Gryllus.   The furci-sternum has been figured in the Coleoptera, but no attempt has been

made to designate it by any especial term, except that Comstock, '04, terms it the antecoxal piece. This, however, is not the antecoxal piece of Comstock, '02, nor of Walton, '00, and most assuredly does not represent the antecoxal plates of Leconte, '61.

In the Blattidæ (pl. III), the furci-sternum of the meso- and meta-thorax is somewhat "T"-shaped, and the internal paired apophyses are borne one at the end of each arm of the "T". Each of the outer openings of the hollow apophyses is covered by a sclerite which may be termed the "tegmentary sclerite" (pl. III, Tg). The function of these "tegmentary" sclerites is doubtless to keep dust, etc., from collecting in the hollows of the apophyses. Miall and Denny, '86, state that there is no ante-furca (*i.e.*, prothoracic furca) in the cockroach; nevertheless paired apophyses which correspond to the meso- and meta-thoracic furca are to be found in the prothorax, if sufficient care be taken in searching for them. The specimen should be slit along the mid-dorsal suture, placed in 10% caustic potash, and left in the paraffin oven until the soft parts can be easily washed away by driving currents of water against them with a pipette. If the soft parts are removed with forceps the apophyses, which are very delicate and somewhat transparent, are usually plucked off before one discovers them. This doubtless accounts for the fact that these structures were not found by Miall and Denny.

The prothoracic furci-sternum of *Nemura* (pl. I, S'_3) is divided into two pieces; in the Trichoptera (fig. 18, S'_3) it is a single plate, drawn out longitudinally, while in the Blattidæ (pl. III, S'_3) it is a somewhat oval transverse sclerite.

In the meso- and meta-thorax, the furci-sternum is frequently separated from the basi-sternum merely by the "intra-sternal" suture. The furci-sternum is usually connected with the katepimeral complex by the narrow antecoxal laterale (fig. 3, L_b), and may likewise be connected with the epimeron by a bridge-like strip extending behind the leg. In the Trichoptera (fig. 18) this strip (S''_3-Em'') dips below the surface of the body, and reappears just before it is joined with the epimeron. In those insects in which the coxal cavity is enclosed posteriorly the coxæ are frequently closely approximated, and that portion of the furci-sternum between them is folded together. This is well shown in the Trichoptera (fig. 18), and in these insects the "pedal region" of the furci-sternum (S''_{3p}) extends along the mesal surface of the coxa, with which it is very closely connected.

It is perhaps of some interest to note that in the Trichoptera the pleural suture is continued in the "coxal suture" (between the meron

and eucoxa), and is extended through the pedal region of the furci-sternum (*i.e.*, the "furcal suture") and up the other side of the insect. With the "intertergal" space (between the postscutellum and the remainder of the tergum) it may separate the segment into two rings, but, from reasons previously given, it is not at all probable that this indicates that the segment is double.

Behind the furci-sternum (S'_3) in *Nemura* (pl. I) are two plates (S'_{3pf}) which may be termed the post-furcal sclerites. These occur in but few insects, and are relatively unimportant.

The Spini-sternum.—Behind the furci-sternum is a smaller sternite, which bears an internal unpaired apophysis, the "spina," and may hence be termed the spini-sternum. This sclerite varies greatly in size and shape, and is never very large.

The prothoracic spini-sternum is the most constant, and occurs in a large number of insects. In the Blattidæ (pl. III, S'_4) it is very long and narrow, while the prothoracic spini-sternum of *Nemura* (pl. I, S'_4) is drawn out transversely into two wing-like processes. In the Trichoptera (fig. 18, S'_4) and Xyelidæ it is very small, and in many insects it is represented only by the endoskeletal "spina" or unpaired pophysis.

The prothoracic spini-sternum (pl. III, S'_4) usually lies just in front of the basi-sternum of the mesothorax, being much nearer to the meso-thorax than to the prothorax. Again, in certain insects (*Corydalis* for example) the mesothoracic spini-sternum is united with the meta-thorax, but in each case the musculature clearly indicates to which segment the sclerite in question belongs.

In the Blattidæ (pl. III, S'''_4) the metathoracic spini-sternum is a distinct sclerite, but in *Nemura* (pl. I, S'''_4) it is united with the furci-sternum, and in most insects it is indistinguishably fused with the latter sternite. As has been mentioned, the præsternum is usually fused with the basi-sternum (except in a few insects such as *Nemura*, *Ectobia*, etc.) and the spini-sternum frequently lies directly in front of the basi-sternum. On this account it would seem very probable that Meinert's, '67, præsternum corresponds to the spini-sternum, rather than the præsternum of Comstock, '02, and the writer. This, however, is mere supposition, and cannot be determined until specimens of *Japyx* can be obtained for dissection.

Amans, '85, divides the sternum into two regions, the ante- and post-sternum. The former of these two regions may possibly correspond to the præ- and basi-sternum, and the latter to the furci- and spini-sternum, but it is impossible to determine this from Amans' descrip-

tions, as he gives no boundaries for his two regions, other than the statement that they are separated by the coxal cavities. His post-sternum is apparently not the same as Meinert's, '67, and is surely not the poststernum of Petri, '99, as the latter sclerite is the meron. Amans' division of the sternum would be of no service in such insects as *Nemura*, or in the Blattidæ, where the coxal cavities do not divide the sternum at all. On this account, and because the sternum is not divided into two but into four sternites, Amans' terminology will not be further considered.

Voss, '04, states that the spini-sternum corresponds to Comstock's, '02, sternellum; but, as we have seen, Comstock's, '02, sternellum is the first abdominal sternum—except in the neck region, where his ster-nellum and sternum are doubtless detached portions of the præsternum. If Comstock had found the four sternal regions, he would doubtless have termed the spini-sternum the poststernellum, as he states (p. 25), "A poststernellum corresponding to the postscutellum has not been observed."

THE INTERSEGMENTALIA.—In front of the laterale, on either side of the mesothorax of such insects as the Trichoptera, Xyelidæ, etc., is a sclerite which is doubtless a detached portion of the laterale. This sclerite may be termed the prælaterale (fig. 18, I_1). Surrounding the spiracle is a number of small plates, the "peritremal sclerites," and between them and the pleuron of the preceding segment is a detached portion of the pleuron, which may be termed the post-pleural sclerite (I_p). All of the above-mentioned sclerites will be included under the general term intersegmentalia, as they lie in the intersegmental membrane, more or less separated from the segment to which they belong.

Voss, '04, claims that the musculature of the first and second thoracic spiracles indicates that they belong to the segment behind which they are situated—that is, that the first is the prothoracic spiracle, and the second is the mesothoracic one. The third spiracle Voss assigns to the first abdominal segment, as do most other investigators.

Heymons, '95, concludes from his embryological studies that the spiracle does not belong to the segment preceding it, but to the segment in front of which it is located. He states that in the early embryonic stages, the primordia of the spiracles lie in the anterior portion of their corresponding segments; as development proceeds, the spiracle may migrate forward and become attached to the segment in front of it, but this is only a secondary modification.

Palmèn, '77, proposed the theory that the first thoracic spiracle may
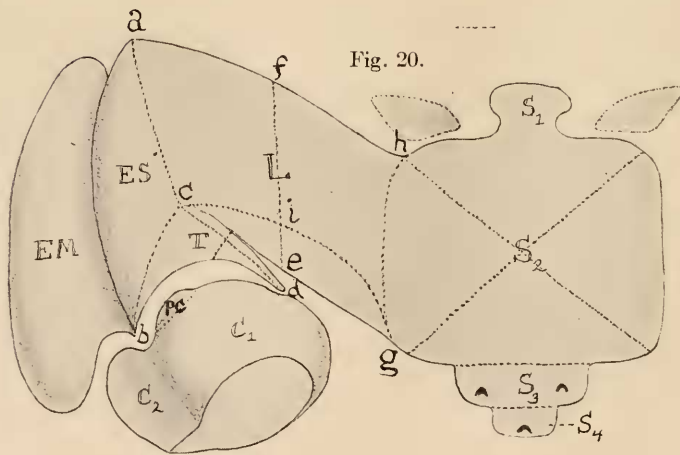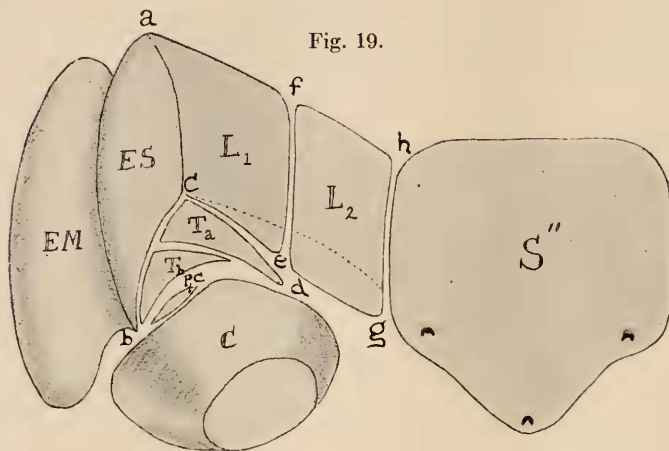
Figs. 19, 20 and 21.—Represent the ventral and lateral sclerites of a segment of the Cursoria (Orthoptera) spread out in one plane. Fig. 20 represents a hypothetical starting point in the formation of the pleural and sternal sclerites of these insects. The dotted lines indicate where divisions may occur. Fig. 19 represents the modification found in the Forficulidæ, and Fig. 21 that found in the Blattidæ. The diagonal lines in the basi-sternum (fig. 21) illustrate the condition found in the prothorax of Ectobia.

Fig. 21.
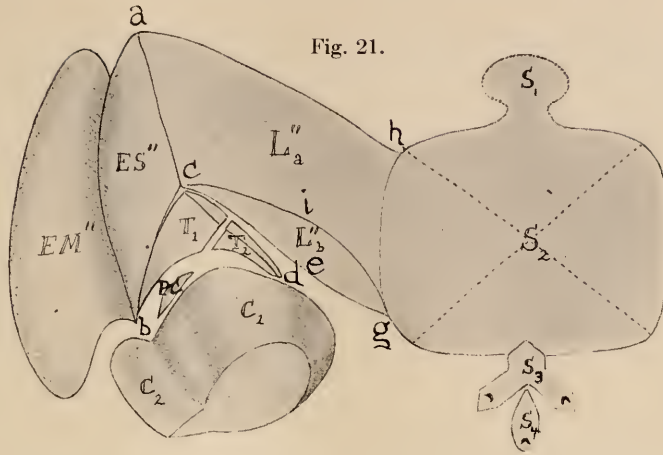
be prothoracic in some insects and mesothoracic in others, but this view does not seem to have a very wide acceptance.

The embryological proof seems to be in favor of Heymons view, and it is certainly the case that the musculature of such insects as the Blattidæ indicates that the spiracles belong to the segment behind them rather than to the preceding one. It is possible, however, to designate the spiracles as the first thoracic spiracle, second thoracic spiracle, etc., without specifying to which segment they belong, and this usage has been here adopted.

In the thorax of *Japyx* there occurs an extra spiracle, which has given rise to much discussion, but all speculation as to its homology can be of no value until the musculature and embryology of *Japyx* have been carefully studied with a view to determining this point.

In insects other than *Japyx*, most investigators now agree in designating the third spiracle as the first abdominal one. It would appear that Latreille's, '20–'22, designating the first abdominal segment the "segment mediaire" is responsible for much of the dispute which later arose concerning this segment, especially in the Diptera and arculeate Hymenoptera; and it is hard to understand why certain modern systematists—Schmiedeknecht, '07, for example—persist in using Latreille's confusing terminology. The first abdominal segment is the first abdominal segment, no matter where it is located, and if it be designated by its proper name, there can be no dispute as to its homology or that of its spiracle.

THE CERVICUM.—Between the head and the prothorax is a narrower neck region whose softer walls give a greater freedom of motion for the head. Embedded in the membranous integument of this region

are a number of plates which serve to strengthen its walls, and furnish an articulation for the head (pl. III, C_{s1}, C_{s2}, etc.).   The number of these sclerites varies greatly, being the most numerous in the Orthoptera, while in certain Coleoptera they are entirely wanting.

The neck region has been designated as the "Mikrothorax" by Verhoeff, '02, who at first considered this as a fourth segment of equal rank with the pro-, meso- and meta-thorax. . There appear to be very grave doubts as to the correctness of this view, and since every investigator who has dealt with this subject terms the region in question the "neck," "Nacken," "cou," etc., according to the language in which the article is written, it seems preferable to designate the neck by the Latin term cervicum—a purely typographical designation, and one which is already implied in the expression "cervical plates," applied to its sclerites for more than eighty years.   As has been stated, Verhoeff, '02, terms the cervicum the "Mikrothorax," and at first considered it a fourth thoracic segment similar to the pro- meso-, and meta-thorax.   Later, however, he designated this "Mikrothorax" as one of the so-called complementary segments ("Vordersegmente") which he states can be found in front of each chief segment of the thorax; and, in addition, he described the remains of an intercalary segment in front of each of the above-mentioned thoracic segments.

In the earlier works there has been much speculation as to the origin of the cervical sclerites, and the question is still a very hotly debated one.

The first of these theories is that of Strauss-Durkheim, '28, who states that in the neck region of the Forficulidæ, one can find traces of the sterna and pleura of two segments formerly existing between the prothorax and the head.   He had thus long ago expressed exactly the same theory, founded upon the same insects, that Verhoeff uses to illustrate his microthorax theory, yet Verhoeff states that "es klingt zwar sonderbar, dass bei den von Hunderten von Forschern studierten Insekten dergleichen (d. h. ein vorn am Thorax befindliches bisher übersehenes segment) noch gefunden werden soll, ist aber tatsächlich so."

The second theory is that of Huxley, '85.   In describing the neck plates he says: "I think it is probable that these cervical sclerites represent the hindermost of the cephalic somites"—in other words, he regards the cervicum as the labial segment.   Comstock, '02, adopts this view, and proposes that the appendages of the cervicum are the second maxillæ which leave their segment and, migrating forward, fuse to form the labium.   He likewise makes use of Carriere's, '98, theory,

that the salivary glands are modified tracheæ, to explain the fact that
the prothorax has no spiracles. Comstock claims that the prothoracic
spiracles are drawn along with the migrating maxillæ and, becoming
united, form the opening of the salivary glands, into which their corre-
sponding tracheæ have changed. He regards the lateral cervicals as
the episternum and epimeron of the labial segment, and the internal
process between these he explains as the endopleural apodeme of this
"segment." Voss, '04, arrived at much the same conclusion from his
study of the musculature, and Riley likewise considers that the cervical
sclerites belong to the second maxillary segment, from his embryological
investigations.

The third theory is that of Newport, '39, who proposes that the
cervical sclerites are detached portions of the prothorax, and repre-
sent the paraptera (laterale?) of the meso- and meta-thorax. Börner,
'03, likewise considers that the cervicals are prothoracic plates which
have become detached from the sternal region of that segment.

In an earlier paper (Crampton, '08) it was suggested that the cervi-
cals possibly correspond to the "intersegmentalia" found between the
pro- and meso-thorax, and that the internal hollow process between the
lateral cervicals might represent the remains of the trunk of a pro-
thoracic trachea. It is quite comprehensible that a strongly chitinized
tracheal stem, such for example as that of a Perlid, could serve as a
muscle support, and, furthermore, it is possible for muscles to become
attached to the tracheæ without interfering with their respiratory
function, as is shown in certain Arachnoidea. In the case of the pro-
thoracic tracheæ, it was proposed that their trunks, being in a favorable
position to serve as a support for the head muscles, were preserved by
a change of function, while the remaining portion of the tracheæ would
be subjected to the same influences which caused the disappearance of
the tracheæ in the buccal somites.

This theory would seem no more improbable than Comstock's, '02,
view that the apodemes of the pro-, meso- and meta-thorax are tra-
cheal vestiges, and is by no means so startling as Carriere's, '98, theory
that the salivary glands are modified tracheæ. Indeed, the views of
Palmèn, '77, Hatschek, '77, Wheeler, '89, and Carriere, '98, who
claim that the tentorium (which likewise serves as a muscle support)
is composed of modified tracheæ, render the theory that the cervical
apodeme is a modified trachea all the more probable; and Palmèn's,
'77, statement that there are traces of a tracheal invagination in the
neck region of the embryo likewise lends weight to the above-men-
tioned theory. However, upon looking into the subject more carefully,

it would appear that these theories dealing with a change of function have not been sufficiently well established, and it would be much simpler to explain the origin of the cervical apodeme as a drawing inward of a portion of the integument (or a corner of one of the sclerites) due to muscular tension.

Even if the theory of the tracheal nature of the cervical apodemes be rejected, this does not preclude the possibility that the peritremal sclerites which lay in front of the prothorax, may have taken part in the formation of the cervical sclerites. The musculature of these plates could admit of such an interpretation, and it would be only natural that such sclerites should be the most developed in the cervical region, where they would serve not only as supports for the attachment of the head muscles, but also as strengthening plates for the membrane of the neck.

Verhoeff's, '02, theory seems very improbable from the fact that no traces of a "mikrothoracic" segment are to be found in the embryo, and none of the segmental structures show any indications of a duplication. On the other hand, if the theory that the cervical sclerites represent the labial segment be accepted, how can one account for the occurrence of similar plates in front of the meso- and meta-thorax, for these surely cannot be likewise interpreted as labial segments?

Voss, '04, attempts to show from the musculature that the cervicum is the labial segment, but it would appear that the cervical muscles are for the most part attached to the occiput, and not to the labium. Furthermore, Riley, '04, himself states that the pleura of the labium are in the occiput region, yet he speaks of the lateral cervicals as the pleurites of the second maxillæ, without giving any reason for thus assigning them to the labial segment.

It is possible that certain detached portions of the labial segment may enter into the formation of the cervical sclerites, but it is not any more correct on this account to designate the cervicum as the labial segment, than it would be to term the intersegmentalia between the first two thoracic segments, the prothorax. The ventral cervical sclerites, termed by Comstock, '02, the labial sternum and sternellum, appear to be detached portions of the prothoracic sternum, while the lateral cervicals may possibly correspond to the "intersegmentalia" between the pro- and meso-thorax, and the dorsal cervicals are probably detached portions of the pronotum.[12]

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[12] In assuming that the cervicals are formed partially from prothoracic sclerites, it must be borne in mind that certain other factors, such as mechanical friction, etc., may have produced certain of these sclerites.

In most Hymenoptera, the prothoracic pleura are very closely con-
nected with the cervical sclerites, and in many insects of this family
the pleura of the prothorax are almost indistinguishably fused with
the lateral cervicals. On this account the term cervico-propleura
has been here applied to the lateral portions of this region in the
Hymenoptera.

If one observe a *Macroxyela* (or a *Tenthredo*), a wasp and an ant,
in the order above mentioned, it may readily be seen that the cervico-
propleura (fig. 13, *C.Pl*) gradually approach one another on the ventral
surface, and almost completely conceal the small prosternum (fig. 14,
S′). In such a case, the ventral portion of the cervico-propleura is
almost without exception incorrectly termed the "prosternum," and
even so careful an observer as Janet, '98, has been deceived in this
respect. Indeed, Rheinhard, '65, terms the entire cervico-propleuron
the prosternum, as does Schmiedeknecht, '07, and a number of
others.

As has been stated, the cervical sclerites may represent the "inter-
segmentalia," and, in addition, certain of the neck plates doubtless
owe their origin to mechanical friction. This brings us to the question
of the formation of sclerites in general. The prevalent opinion is that
the segments originally consisted of chitinized rings, which became
split between the pleura and tergal region to accommodate the wing;
and the pleura became separated from the sternal region to make room
for the leg. This view, however, is not borne out by the facts of onto-
genetic development, nor by the results of comparative morphological
study. In all of the very active larvæ studied, the sclerites of the ster-
num and pleura form as islands (pl. IV) which later unite to form the
chitinous integument. Again, in the adult stages of the lowest insects,
such as *Japyx* for example, even though there are no wings present, the
segments are not solid rings interrupted only at the base of the leg;
but consist for the most part of small individual sclerites. It is like-
wise the case that within the same family the sclerites of the general-
ized forms are more numerous and distinct, while in the more specialized
forms there is a marked tendency toward a fusion of the sclerites to
form a solid ring; and even the segments themselves tend to become
closely united.

With regard to the origin of the sclerites, there are a number of fac-
tors which might give rise to such chitinous plates. Among the chief
of these causes is doubtless the stimulus of muscular tension, which
would serve to produce a chitinized thickening of the integument at
the points of origin and insertion. The sclerites thus formed would not

only serve as firmer supports than the softer yielding integument about them, but would likewise serve as protective plates. Contact with external objects and mechanical irritation, such, for example, as the rubbing of one part upon another, doubtless play no inconsiderable rôle in the production of the sclerites. This was well illustrated in the case of a young cricket, whose developing wing pads, by rubbing on the tergum upon which they rested, left their outlines distinctly imprinted in its integument.

In addition to the formation of chitinous areas in the integument, by the stimulus of its tension, muscular stress may likewise bring about the breaking up of the large chitinous plates, or cause their division into smaller regions by producing the infolding of hollow ridges, as is shown in the tergum[13] and pleura. Again, it is quite evident that portions of chitinous regions may become detached by muscular tension and drawn into another region, as is shown in the case of the "migration" of the meron; such instances, however, are very rare, and this method would consequently play an unimportant rôle in sclerite formation.

However, the method of sclerite formation, the theories of segmental duplication, etc., are questions of minor interest, as the purpose of this paper is to deal with the comparison of the sclerites in the adult insect. With regard to the homologizations and terminology at present in vogue, it may readily be seen that entomologists are by no means agreed in these matters. Furthermore, the views here set forth frequently differ very radically from those of other investigators, and on this account the following list, which to some extent anticipates certain points which will be brought out in a subsequent publication, may be of some service, not only to furnish a résumé of the synonyms, etc., applied to the various sclerites, but also to give a brief outline of the results here reached :—

The Thorax.

Thorax—Thorax (Nitzsch, '18).
      It is composed of the pro-, meso- and meta-thorax.
      The "thorax" of Strauss-Dürkheim, '28, is the meso- plus the meta-thorax. Kirby, '28, following Fabricius, Linné and the other earlier writers, restricts the term thorax to the notum or tergum, but these obsolete usages need not be further discussed here.
Prothorax (')[14]—Prothorax (Audouin, '20).
      = Protothorax (Nitzsch, '18).

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[13] It is quite uncertain whether the postscutellum was separated from the remainder of the tergum by muscular tension, or whether the postscutellum was originally itself a distinct sclerite.

[14] The signs given in parentheses refer to the method of indicating the region in question in the different figures.

= Collum (Knoch, 1801).
= Corselet (Strauss-Dürkheim, '28).
= Collier (Chabrier, '20).
= Manitruncus (Kirby, '28).
Verhoeff's, '04, "proterothorax" is the prothorax plus the cervicum.
Mesothorax (″)—Mesothorax (Nitzsch, '18).
Metathorax (‴)—Metathorax (Nitzsch, '18).
The meso- plus metathorax = Knoch's, 1801, pectus.
= Chabrier's, '20, tronc alifère.
= Kirby's, '28, alitruncus.
= Strauss-Dürkheim's, '28, "thorax."
Verhoeff's, '04, "deuterothorax" = the mesothorax plus the metathorax and intersegmentalia.

THE SEGMENT.

Tergum (N)—Tergum (Audouin, '24).
= Notum (Burmeister, '32).
Escherisch's ('06) "mesonotum" (which, according to Burmeister, '32, means the notum or tergum of the mesothorax) is the mesothoracic scutum.
Pleuron (Pl)—Pleuron (Amans, '85).
= Pleura (Audouin, '24).
Kirby's, '28, "pleura" is the epimeron.
Burmeister's, '32, "pleura" is the episternum.
Sternum (S)—Sternum (Audouin, '24).
The sternum of Comstock, '05, is the basisternum. That of Comstock, '02, is the basi- plus furci-sternum, except in the cervical region, where it is doubtless a portion of the præsternum.

THE TERGUM.

(For example, that of the Mesothorax.)

Præscutum (N''_1)—Præscutum (Audouin, '32).
(The other uses of the word præscutum are given under the heading Mediscutum.)
= Proterophragma (Kleuker, '83).
= Antedorsum (Amans, '85). In the Diptera, Amans', '85, and Petri's, '99, antedorsum is the mediscutum.
Scutum (N''_2)—Scutum (Audouin, '32).
Voss', '04, scutum is the scutum plus the scutellum. The scutum of Hammond, '81, Künkel, '75–'81, Brauer, '82, Lowne, '90–'92, Packard, '98, Hewitt, '07, a. o., is the parapsidoscutum.
= Dorsum (Amans, '85).
(According to Audouin, '32, the term dorsum refers to the whole dorsal surface of the insect.)
In the Diptera, Amans', '85, and Petri's, '99, "dorsum" is the parapsidoscutum.
Mediscutum (N''_2a)—Mediscutum (Crampton, '08).
= The præscutum of Hammond, '81, Künkel, '75–'81, Brauer, '82, Lowne, '90–'92, Packard, '98, Hewitt, '07, a. o.
= Escherisch's, '06, "mesonotum."
Parapsidoscutum (N''_2b)—Parapsidoscutum (Crampton, '08).
= In part the parapsides of MacLeay, '30.
= The scutum of Hammond, '81, a. o.
= Escherisch's, '06, proscutellum of the mesothorax (but according to Audouin, '24, the term proscutellum refers to the prothoracic scutellum alone).
= Emery's, '00, "paratteri" (i.e., parapsides?).
Pterygoda (Pt)—"Pterygodes" (Latreille, '20–'22).
= Tegulæ (Kirby, '28).

     = Squamulæ (MacLeay, ʼ30).
     = Hypoptere (Audouin, ʼ25).
     = Paraptere (Audouin, ʼ25).
     Hammond's parapteron is the anepisternum.
     = "Hautpolster" (Voss, ʼ04).
SCUTELLUM (N''_3)—SCUTELLUM (Audouin, ʼ24).
     = Postdorsum (Amans, ʼ85).
POSTSCUTELLUM (N''_4)[15]—POSTSCUTELLUM (Audouin, ʼ24).
     = Subpostdorsum (Amans, ʼ85).
     = Part of Kleukers, ʼ83, deuterophragma.
     = "Postscutum" (Voss, ʼ04).
     Brauer, ʼ82, regards the upper portion of the dipteran postscutellum as the
       entire postscutellum, and terms its lower portion the "phragma."
MEDIOPHRAGMITE (N''_{4}a)—MEDIOPHRAGMITE (Crampton, ʼ08).
PLEUROPHRAGMITE (N''_{4}b)—PLEUROPHRAGMITE (Crampton, ʼ08).
     The mesothoracic pleurophragmite is Lowne's, ʼ90–ʼ92, "lateral plate of
       the metathorax."
     The mesothoracic pleurophragmite is Brauer's, ʼ82, " ? Episternum des
       Metathorax"—"wahrscheinlich der Rest des Præscutums des Metathorax
       und zwar homolog mit der Ecke vor der Flügelwurzel."
     = Hammond's, ʼ81, "uncertain plate."
     = Petri's, ʼ99, metathoracic antepleura (*i.e.*, episternum). The piece in
       question, however, belongs to the mesothorax.
     = Osten-Sacken's, ʼ64, "metapleura" (the term metapleura refers to the
       pleura (*i.e.*, epimera and episterna) of the metathorax).
PARAPLEURON (N'''_{4}bb)—PARAPLEURE (Kolbe, ʼ93).
     Knoch's, 1801, "parapleurum" is the epimeron.
     Cuvier's, ʼ28, "parapleure" is the epimeron.
     Kirby's, ʼ28, "parapleura" is the epimeron.
     Burmeister's, ʼ32, "parapleura" is the episternum.
     Fieber's, ʼ61, "parapleurum" is the epimeron.
     Voss, ʼ04, "parapleura" is the episternum.
     Lacordaire's, ʼ54, "parapleures" are the epimera and episterna.

THE PLEURON (OF THE MESOTHORAX).

EPIMERON (*Em''*)—EPIMERON (Audouin, ʼ24).
     = Pleurit (Heymons, ʼ99).
     = Parapleura (Kirby, ʼ28, a. o.).
     = Pleura (Burmeister, ʼ32, a. o.).
     = Anopleure (Verhoeff, ʼ03).
     = Postpleuron (Amans, ʼ85).
     Petri's, ʼ99, mesothoracic "postpleura" is the anepimeron. On the other
       hand, his metathoracic "postpleura" is the anepisternum. Lowne's, ʼ90–ʼ92,
       epimeron is the katepimeron. Brauer's, ʼ82, epimeron is the anepimeron.
     Hammond's, ʼ81, epimeron is the meron.
     Sharp's, ʼ95–ʼ99, "epimeron?" in his figure of *Blabera*, is the trochantinus
       major.
ANEPIMERON (*EM''*a)—ANEPIMERON (of this paper).
     = Hyperepimeron (Crampton, ʼ08).
     = Lowne's, ʼ90–ʼ92, episternum.
     = Brauer's, ʼ82, entire epimeron. The anepimeron of the mesothorax,
       Petri, ʼ99, terms the postpleura (*i.e.*, epimeron), but his metathoracic
       postpleura is the anepisternum.
KATEPIMERON (*EM''*k)—KATEPIMERON (of this paper).
     = Hypoepimeron (Crampton, ʼ08).
     = Lowne's, ʼ90–ʼ92, entire epimeron.
     The katepimeron of the mesothorax, Petri, ʼ99, terms the metathoracic
       antesternum.

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[15] According to Snodgrass, ʼ08, Verhoeff's pseudonotum and Berlese's acro-
tergite of the first abdominal segment are homologous with the postscutellum.

EPISTERNUM (ES'')—EPISTERNUM (Audouin, '24).
    = Parapleura (Burmeister, '32).
    = Pleura (Kirby, '28).
    = Coxopleure (Verhoeff, '03) in *Forficula*. In the Blattidæ, Verhoeff's coxopleure is the episternum plus the anterior laterale.
    Comstock's, '02, and Walton's, '00, episternum in the Blattidæ is the episternum plus the anterior laterale.
    Lowne's, '90–'92, episternum is the anepimeron.
    Brauer's, '82, episternum is the katepisternum.
ANEPISTERNUM (ES''_a)—ANEPISTERNUM (of this paper).
    = Hyperepisternum (Crampton, '08).
    = Lowne's, '90–'92, "lateral plate."
    = The episternum of Brauer, '82, a. o.
    = Hammond's, '81, parapteron.
    = Petri's, '99, antepleura of the mesothorax. On the other hand, his metathoracic antepleura is the mesothoracic pleurophragmite.
KATEPISTERNUM (ES''_k)—KATEPISTERNUM (of this paper).
KATEPISTERNAL COMPLEX (ES''_x)—KATEPISTERNAL COMPLEX (of this paper).
LATERALE (L'')—LATERALE (Crampton, '08).
    = Voss, '04, coxosternum.
    Börner's, '03, coxosternum is the epimeron, episternum and laterale.
    Verhoeff's, '97, coxasternum is the fusion product of the sternum and coxæ.
ANTERIOR LATERALE (La)—ANTERIOR LATERALE (of this paper).
ANTECOXAL LATERALE (L_b)—ANTECOXAL LATERALE (Crampton, '08).
    = "Antecoxal piece" (Walton, '00).
    Comstock's, '02. "antecoxal piece" is the antecoxal trochantin.
    Comstock's, '05, "antecoxal piece" is the furci-sternum.
    Leconte's, '61–'62, "antecoxal plates" are the lateral cervicals.
    = Second antecoxal piece (Comstock, '02).
    = Verhoeff's, '03, katopleure in the Blattidæ. On the other hand, his katopleure in the Dermiptera is the episternal laterale. In the prothorax of Echinosoma, his katopleure is the sternal laterale. Börner's,'03, katopleure in the mesothorax of *Anisolabis* is the episternal and sternal laterale. In prothorax of *Anisolabis* it is the sternal laterale and the posterior lateral cervicals. In the Blattidæ his katopleure is the antecoxal laterale.
EPISTERNAL LATERALE (L''_1)—EPISTERNI-LATERALE (Crampton, '08).
    = Verhoeff's, '03, katopleure in the Dermiptera. In the Blattidæ, however his katopleure is the antecoxal laterale.
STERNAL LATERALE (L''_2)—STERNI LATERALE (Crampton, '08).
    = Verhoeff's, '03, "Vorplatte" of the mesothorax in the Blattidæ. In the Blattid prothorax his "Vorplatte" is a lateral cervical.
TROCHANTINUS (T)—TROCHANTINUS (MacLeay, '30).
    = Trochantine (Audouin, '24).
    = Rotule (Strauss-Dürkheim, '28).
    = Præcoxal plate (Voss, '04).
ANTECOXAL TROCHANTIN (T_a'')—ANTECOXAL TROCHANTIN (Crampton, '08).
    = Antecoxal piece (Comstock, '02).
    The other usages of the term antecoxal piece are given under the term antecoxal laterale.
COXAL TROCHANTIN (T_b'')—COXAL TROCHANTIN (Crampton, '08).
    = Comstock's, '02, entire trochantinus.
TROCHANTINUS MAJOR (T'_1)—TROCHANTINUS MAJOR (Crampton, '08).
    = Sharp's "epimeron?" in Blabera.
TROCHANTINUS MINOR (T'_2)—TROCHANTINUS MINOR (Crampton, '08).
    = Sharp's entire trochantinus in *Blabera*.
EUCOXA (C''_1)—EUCOXA (Verhoeff, '04).
    = Coxa genuina (Walton, '00).
MERON (C''_2)—MERON (Walton, '00).
    Börner's, '03, meron is the epimeron, episternum and laterale.
    = Metacoxa, Verhoeff, '04.
    The term metacoxa means the coxa of the metathorax.

Petri's, '99, poststernum of the mesothorax is the meron.   On the other hand, his metathoracic poststernum is the katepimeron.

Brauer's, '82, Lowne's, '90–'92, and Hewitt's, '07, sternum of the dipteran metathorax is the mesothoracic meron.

According to Packard, '98, the meron is the trochantinus, while Sharp, '95–'99, designates it as a fold of the epimeron.

STERNUM (S'')—STERNUM (Audouin, '24).

The sternum of Comstock, '02, is the basi- and furci-sternum, except in the cervical region where it is doubtless a detached portion of the præsternum. Comstock's, '05, sternum is the basi-sternum.

Brauer's, '82, mesosternum is the mesothoracic katepisternal complex, the laterale and the basisternum.   On the other hand, his metasternum is the mesothoracic meron.

Petri's, '99, antesternum of the mesothorax is likewise the katepisternal complex, laterale and basisternum (as in the case with Lowne's, '90–'92, "plastron," and Osten-Sacken's, '64, "sternopleura"); his metathoracic antesternum, however, is the mesothoracic katepimeron.

PRÆSTERNUM (S''_1)—PRÆSTERNUM (Comstock, '02).

Meinert's, '67, præsternum is probably the spinisternum.

BASISTERNUM (S''_2)—BASISTERNUM (Crampton, '08).

FURCISTERNUM (S''_3)—FURCISTERNUM (Crampton, '08).

= Comstock, '04, "antecoxal piece."

SPINISTERNUM (S_4)—SPINISTERNUM (Crampton, '08).

CERVICUM (Cs)—CERVICUM (Crampton, '08).

= Mikrothorax (Verhoeff, '02).

BIBLIOGRAPHY.

1880.   ADOLPH.   Ueber Insektenflügel. Nov. Act. Abh. d. k. Leop. Carol. deutsch-Akad. d. Naturf., Bd. XLI, 2.

1885.   AMANS.   Comparaison des organes du vol dans la série animale.   Ann. Sci. Nat., VI sér., Zool., T. XIX.

1820.   AUDOUIN.   L'anatomie comparative des parties solides des insectes. Présentée par M. Cuvier.   Ann. Gen. Sci. Phys., T. VII.

1824.   ——.   Recherches anatomiques sur le Thorax des animaux articulés. Ann. Sci. Nat., T. I, sér. 1.

1825.   ——.   Article "Insectes," dans la Dictionnaire Classique d'Histoire Naturelle dir, par Bory de Ste. Vincent, Paris, T. VIII.

1832.   ——.   Exposition de l'anatomie du Thorax.   Par W. S. MacLeay Accompagnée de Notes par M. Audouin.   Ann. Sci. nat., T. XXV, sér. 1

1884.   AYERS.   On the Development of Œcanthus niveus.   Mem. Boston Soc Nat. Hist., Vol. III.

1826.   v. BAER.   Ueber das Aussere u. innere Skelett der Insekten.   Meckel's Archiv. Anat. Physiol.

1880.   BALFOUR.   Handbuch der vergl. Anat.

1893.   BANKS.   Notes on the Mouth Parts and Thorax of Insects.   Am. Nat.

1904.   ——.   Notes on the Structure of the Thorax and Maxillæ of Insects. Proc. Ent. Soc. Washington, Vol. VI.

1882.   BERLESE.   Osservazioni sulla anatomie del Gryllus campestris.   Atti Soc. Veneto Trent, Padova, Vol. VII..

1890.   v. BENSDORFF.   Ableitung der skulpturverhältnisse bei Coleopteren-flügeln.   Zool. Anz., 13 Jahrg.

1902.   BÖRNER.   Die Gliederung der Laufbeine der Atelocerata. Sitzbr. Gesell. Natf. Fr. Berlin, No. 9.

1903a.   ——.   Ueber die Beingliederung der Arthropoden. Ibid., Nr. 7.

1903b.   ——.   Kritische Bemerkungen über einige Vergleichendmorpholo-gische Untersuchungen K. W. Verhoeff's.   Zool. Anz., Bd. 26.

1904.   ——.   Zur Klärung der Beingliederung der Ateloceraten. Zool. Anz., Bd. 27.

1899.   BORDAGE.   Probable mode of formation of the fusion between Femur and Trochanter in Arthropoda.   Ann. Mag. Nat. Hist., Vol. III.

1882. BRAUER. Ueber das Segment médiaire Latreille. Sitzb. Kais. Akad. Wiss. Wien.-Math. Nat. Klasse, Bd. LXXV, Abt. I.

1885. ——. Systematisch-Zoologische Studien. *Ibid.*, Bd. XCI, Abt. I.

1903. BREED. The changes which occur in the muscles of a Beetle, Thymalus marginicollis, during metamorphosis. Bull. Mus. Comp. Zool. Cambridge, Vol. XL, No. 7.

1890. BRONGNIART. Note sur quelque insectes fossiles du terrain houiller presentent au prothorax des appendices aliformes. Bull. Soc. Philom., T. II, 8ᵉ Sér.

1882. BROOKS. Handbook of Invertebrate Zoology. Boston.

1832. BURMEISTER. Handbuch der Entomologie. Berlin.

1869. BRANDT. Beiträge zur Entwicklungsgeschichte der Libelluliden und Hemipteren. Mém. Acad. St. Petersb., 7. Sér., T. 13, No. 31.

1870. BUETSCHLI. Zur Entwicklungsgeschichte der Biene. Zeit. Wiss. Zool., Bd. XX.

1890a. CARRIERE. Die Embryonalentwicklung von Chalicodoma muraria. Zoll. Anz., Jahrg. 13.

1890b. ——. Die Entwicklung der Mauerbiene. Arch. Mik. Anat., Bd. XXXV.

1898. CARRIERE and BUERGER. Die Entwicklungsgeschichte der Mauerbiene im Ei. Nova. Acta Abh. Kais. Leop. Carol. Akad. Naturf. Halle, Bd. LXIX.

1886. CHOLODKOWSKY. Zur Morphologie der Insektenflügel. Zool. Anz., 9. Jahrg.

1887. ——. Ueber die Prothorakalanhänge der Lepidopteren. Zool. Anz., Jahrg. 13.

1891. ——. Die Embryonalentwicklung von Blatta germanica.

1889. ——. Studien zur Entwicklungsgeschichte der Insekten. Zeit. Wiss. Zool., Bd. 48.

1820. CHABRIER. Essai sur le vol des Insectes. Mém. Mus. Hist. Nat.,Paris,T. 7.

1822. ——. Essai sur le vol des Insectes. *Ibid.*, T. 8.

1898–99. COMSTOCK and NEEDHAM. The Wings of Insects. Am. Nat., Vol. 22 and 23.

1902. COMSTOCK and KOCHI. The Skeleton of the Head of Insects. *Ibid.*, Vol. 36.

1904. COMSTOCK and COMSTOCK. A Manual for the Study of Insects. Ithaca.

1853. CORNELIUS. Beiträge zur nähren Kenntnis von Periplaneta orientalis. Elberfeld.

1908. CRAMPTON. Ein Beitrag zur Homologie der Thorakal-Sklerite der Insekten (Kapitel II). Inaug. Diss., Berlin.

1823. CUVIER. Rapport sur les recherches anatomiques sur le thorax des animaux articules, ... par M. Audouin. Paris.

1828. ——. Les Insectes; dans le Règne animal, Vol. I.

1841. DUFOUR. Recherches anatomiques et physiologiques sur les Orthoptères . . . . Mem. Acad. Roy. Sci. Institut de France, T. VII, sér. 2.

1907. DUERKEN. Die Tracheenkiemenmuskulatur der Ephemeriden. . . . Zeit. Wiss. Zool., Bd. 87.

1900. EMERY. Intorno al Torace delle Formiche. Bull. Soc. Ent. Ital., 32.

1903. ENDERLEIN. Ueber die Morphologie . . . . der Corrodentien. Zool. Anz., Bd. 26.

1838–39. ERICHSON. Die Käfer der Mark Brandenburg. Berlin.

1906. ESCHERICH. Die Ameise. Braunschweig.

1820. ESCHSCHOLTZ. Beschreibung des inneren skeletts einiger Insekten aus Verschiedenen Ordnungen. Panders Beiträge zur Naturkunde aus den Ostseeprovinzen Russlands.

1896. FABRE. Etudes sur les Locusteens. Ann. Sci. Nat. Zool., sér. 8, T. I.

1861. FIEBER. Die europäischen Hemiptera nach der analytischen Methode bearbeitet. Wien.

1899. FOLSOM. The Segmentation of the Insect Head. Psyche, Vol. 8.

1900. ——. The Development of the Mouth-parts of Anurida maritima. Bull. Mus. Comp. Zool., Vol. 36.

4

1877. GRABER. Die Insekten. München.
1881–83. GOSCH. On Latreille's Theory of le segment médiaire. Naturh. Tidsk. Kjöbenhavn. III Roekke. 13 Bind.
1887. GRASSI. Anatomia comparata dei Tisanuri. Atti Real. Acad. Lincei, 4 sér., Vol. IV.
1832. GRIFFITHS. Insects, Animal Kingdom.
1903. GRUENBERG. Die Homologie des Trochanters bei Chilopoden u. Insekten. Sitz. Ber. Gesell. Naturf. Berlin.
1886. HAASE. Die Prothorakalanhänge der Insekten. Zool. Anz. and Jahrg.
1889a. ——. Die Zusammensetzung des Körpers der Schaben. Sitzb. Berlin. Gesellsch. Naturf., No. 6.
1889b. ——. Zur Anatomie der Blattiden. Zool. Anz., No. 303.
1889c. ——. Die Abdominalanhänge der Insekten mit Berücksichtigung der Myriopoden. Morph. Jahrb.
1889. HAGEN. Ueber die früheren Zustände der Libellen nebst Andeutung über Bildung des Thorax. Stetiner Entom. Zeit., 5. Jahrg.
1881. HAMMOND. On the Thorax of the Blow-fly. Jour. Linn. Soc. London, Zoology, Vol. 15.
1906–8. HANDLIRSCH. Die fossilen Insekten. Leipzig.
1893. HANSEN. Zur Morphologie der Gliedmassen u. Mundteile bei Crustaceen u. Insekten. Zool. Anz., Bd. 16.
1894. ——. On the Structure and Habits of Hemimerus talpoides. Ent. Tidsk., Arg. 15.
1907. HEWITT. The Structure, Development and Binomics of the House-fly. Quart. Jour. Mic. Sci., No. 203.
1823. HEUSINGER. Vorvort u. Nachschrift zum Aufsatz von T. Thon über das Skelett der Käfer. Meckels. Archiv. f. Anat. U. Physiol, Abh. 20, Bd. 8.
1889. HEIDER. Die Embryonalentwicklung von Hydrophilus piceus. Theil I. Jena.
1895a. HEYMONS. Die Segmentierung des Insektenkörpers. Anhang Abh. Kgl. preuss. Akad. Wien.
1895b. ——. Die Embryonalentwicklung von Dermipteren u. Orthopteren. Jena.
1899. ——. Beiträge zur Morphologie u. Entwicklungsges. der Rhynchoten. Abh. K. L. Carol. Deutsch. Akad. Naturf., Bd. 74, No. 3, Halle.
1885. HUXLEY. A Manual of the Anatomy of Invertebrated Animals. New York.
1895. JANET. Sur les muscles des fourmis, des guespes et des abeilles. Compt. Rend. Acad. Sci., T. CXXI.
1898. ——. Anatomie du corselet de la Myrmica rubra reine. Mém. Soc. Zool. d. France, T. XL.
1896. JAWOROWSKI. Die Entwicklung des Spinnapparates bei Trochosa sig-noriensis mit Berucksichtigung der Abdominalanhänge und der Flügel bei den Insekten. Jen. Zeit Naturw., Bd. 30.
1897. ——. Zu meiner extremitaten u. Kiementheorie bei Anthropoden. Zool. Anz., 20 Jahrg., No. 532.
1888. JORDAN. Anatomie u. Biologie der Physopoden. Zeit Wiss. Zool., Bd. XLVII.
1888. JOURDAIN. Sur le Machilis maritima. C. R. Acad. Sci., T. CVI.
1820. JURINE. Observations sur les ailes des Hymenoptères. Mém. reale. Acad. Sci. Torino, Tome XXIV'
1828. KIRBY and SPENCE. Introduction to Entomology. Vol. 3.
1883. KLEUKER. Ueber Endoskeletale Bildungen bei Insekten. Diss. Dorpat. Göttingen.
1801. KNOCH. Neue Beiträge zur Insektenurkunde. Leipzig.
1893. KOLBE. Einführung in die Kenntnisse der Insekten. Berlin.
1901. ——. Vergleichend-morphologische Untersuchungen bei Coleopteren. Arch. f. Naturg., 67 Jahrg., Beiheft.
1885. KOROTNEFF. Die Embryologie der Gryllotalpa. Zeit. Wiss. Zool., Bd. XLI.
1890–92. KORSCHELT U. HEIDER. Lehrbuch der Vergl. Entwicklungsges. der wirbellosen Tiere. Jena.

1898. KRUEGER. Ueber die Entwicklung der Flügel der Insekten mit besonder Berücksichtigung der Deckflügel der Käfer. Inaug. Diss. Göttingen.

1875–81. KUENKEL D'HERCULAIS. Recherches sur l'organisation et le developpement des Volucelles. Paris.

1834–38. LACORDAIRE. Introduction a l'éntomologie. Paris.

1854. ——. Genera des Coleoptères. Paris.

1900. LAMEERE. Notes pour la classification des Coleoptères. Ann. Soc. Ent. Belg., T. XLIV.

1866. LANDOIS. Anatomie des Hundflohs. Nova. Acta. Acad. Leop. Carol. Dresden., Bd. XXXIII.

1867. ——. Die Tracheenverschluss bei den Insekten. Zeit. Wiss. Zoll., Bd. XVII.

1820–22. LATREILLE. Des rapports géneraux de l'organisation extérieure des animaux invertebres articules. Mém. Mus. Hist. Nat., T. VI–VII.

1831. ——. Cours d'Entomologie. Paris.

1861–62. LECONTE. Classification of the Coleoptera of North America. Smithsonian Miscellaneous Collections, Part I; also Leconte and Horn, Washington, 1883.

1847. LEIDY. History and Anatomy of the Hemipterous genus Belostoma. Jour. Acad. Nat. Sci. Phila., Vol. 1 (N.S.), Part I.

1881. v. LENDENFELD. Der Flug der Libellen. Sitzb. K. K. Akad. Wiss. Wien. Math. Naturw. Klasse. Jahrg. 4, Bd. LXXXIII, Abt. I.

1873. LIEBE. Die Gelenke der Insekten. Programm d. Kgl. Gymnasiums zu Chemnitz, 4.

1864. LINDEMANN. Notizen zur Lehre vom äusseren Skelette der Insekten. Bull. Soc. Imp. Moscau, T. XXXVII, Part I.

1861. LÖW. Beiträge zur Kenntnis der Orthopteren. Verh. Zool. Bot. Gesell. Wien, Bd. XI.

1890–92. LOWNE. The Anatomy, Physiology, Morphology and Development of the Blow-fly. London (also 1870).

1881. LUBBOCK. On the Anatomy of Ants. Trans. Linn. Soc. London, 2 ser., Vol. 2, Zool., Part 2.

1883. LUKS. Ueber die Brustmuskulatur der Insekten. Jen. Zeit. Naturw. u. Med., Bd. XVI.

1906. MACGILLEVRAY. A Study of Wings of the Tenthredinoidæ. Proc. U. S. Nat. Mus., Vol. XXIX.

1830. MACLEAY. Explanation of the Comparative Anatomy of the Thorax in Winged Insects. Zool. Jour. London, Bd. V, No. XVIII.

1832. ——. French translation; see Audouin, '32.

1862–63. MEINERT. Anatomia forficularum. Diss. Med. Hofn., Kopenhagen.

1867. ——. On the Campodea, a Family of Thysanura (translation). Ann. and Mag. Nat. Hist. London, III Ser., Vol. 20.

1880. ——. Sur l'homologie des élytres des Coleoptères. Entom. Tidskr. Stockholm, Bd. I.

1886. MIALL and DENNY. The Structure and Life History of the Cockroach. London.

1897. MIALL and SHELFORD. The Structure and Life History of Pchalacrocera replicata. Trans. Ent. Soc. London.

1900. ——. The Structure and Life History of the Harlequin-fly. Oxford.

1871–73. MUELLER. Beiträge zur Kenntnis der Termiten. Jen. Zeit. Med. u. Naturwiss, Bd. 7 and 9.

1833–34. NEWMAN. Osteology or External Anatomy of Insects. Entom. Mag., Vol. I–II.

1839. NEWPORT. Insects. Todd's Cyclopædia of Anatomy and Physiology, Vol. II.

1818. NITZSCH. Die Familien u. Gattungen der Tierinsekten. Magazin der Entomologie, herausgegeben von Germar, Halle, Bd. III.

1884. OSTEN-SACKEN. An Essay on Comparative Chætotaxy. Trans. Ent. Soc. London.

1898. PACKARD. Textbook of Entomology. New York.

1877. PALMÈN. Zur Morphologie des Tracheensystems. Leipzig.

1890. PATTEN. On the Origin of Vertebrates from Arachnids. Quart. Jour. Micr., Vol. 31, N. S., Part 3.

1899. PETRI. I muscolo delle ali nel ditteri e negli imenotteri. Bull. Soc. Ent. Ital., 31.

1832. RATHKE. Zur Entw. Gesch. von Blatta germanica. Meckel's Archiv. f. Anat. and Physiol., Bd. 6.

1844. ——. Zur Entw. ges. der Maulwurfsgrille. *Ibid.*

1886. REDTENBACHER. Vergl. Studien über das Flugelgeäder der Insekten. Ann. d. Hofmuseums Wien, Bd. I.

1886. REHBERG. Ueber die Entwicklung des Insektenflügels an Blatta germanica. Jahresb. Kgl. Gymnasiums zu Marienwerder, Schuljahr 1885–86.

1865. REINHARD. Zur Ent. ges. des Tracheensystems der Hymenopteren. Berliner Anatom. Zeitschr., Jahrg. 9.

1892. RILEY. Tegulæ and Patagia of Lepidoptera. Proc. Ent. Soc. Washington, Vol. II.

1904. RILEY. The Embryological Development of the Skeleton of the Head of Blatta. Am. Nat., Vol. 38.

1860. SAMUELSON and HICKS. The Earthworm and the Common House-fly. London.

1879. SAUSSURE. Études sur l'aile des Orthoptères. Ann. Sci. Nat., 6 sér., 7 X.

1816. SAVIGNY. Mémoires sur les Animaux sans vertébres. Paris.

1907. SCHMIEDEKNECHT. Die Hymenopteren Mitteleuropas. Jena.

1895–99. SHARP. Insects. Cambridge Natural History, Vols. V–VI, London.

1896. ——. The so-called Secondary Wing of Coleoptera. Trans. Ent. Soc. London.

1902. SILVESTRI. Einige Bemerkungen über den sogenannten Mikrothorax der Insekten. Zool. Anz., Nr. 680, Bd. 25.

1908. SNODGRASS. A Comparative Study of the Thorax in Orthoptera, Euplexoptera and Coleoptera. Proc. Ent. Soc. Wash., Vol. IX.

1843. SPINOLA. Considerazione sopra i costumi degli Imenotteri del genere Sirex.

1828. STRAUSS-DUERKHEIM. Considerations géncrales sur l'anatomie comparée des animaux articulés. Paris.

1903. TOWER. The Origin and Development of the Wings of Coleoptera. Zool. Jahrb., Abt. f. Ontogenie u. Phys., Bd. XVII.

1898. UZEL. Studien über die Entwicklung der apterygoden Insekten.

1893. VERHOEFF. Vergleichende Untersuchungen über die Abdominalsegmente der weiblichen Hemiptera, Heteroptera und Homoptera. Verh. Naturw. Ver. Preuss. Rheinlande Westfalen. Reg. Bez. Osnabrück, Jahrg. 50, Bonn.

1895. ——. Cerci und styli der Tracheaten Entom. Nachrichten.

1897. ——. Bemerkungen über abdominale Korperanhänge bei Insekten u. Myriopoden. Zool. Anz., Bd. 20.

1902a. ——. Ueber Dermipteren . . . . und über den Mikrothorax der Insekten. Zool. Anz., Bd. 25, No. 665.

1902b. ——. Ueber die Nerven des Metacephalsegmentes und die Insektenordnung Oothecaria. Zool. Anz., Bd. 25, No. 685.

1903a. ——. Beiträge zur vergl. Morphologie des Thorax der Insekten mit Berücksichtigung der Chilopoden. Nova acta K. L. C. deutschen Akad. Naturf., Bd. LXXXI, No. 2, Halle.

1903b. ——. Vergleichende Morphologie der Laufbeine der Opisthogoneata. *Ibid.*

1903c. ——. Ueber den Thorax der Insekten mit besonderer Berücksichtigung des Mikrothorax und der Pleuren. *Ibid.*

1903d. ——. Ueber Tracheaten Beine. 2. Aufsatz. Zool. Anz., Bd. 26, Nr. 692.

1903e. ——. Ueber Tracheaten Beine. 3. Aufsatz. Sitzb. Gesell. Naturf Fr. Berlin, Heft 2.

1903f. ——. Ueber Tracheaten Beine. 4. Aufsatz. Nova acta, Bd. LXXXI, No. 4.

1903g. ——. Intercalarsegmente der Chilopoden. Arch. f. Naturg.

1904a. ——. Ueber Tracheaten Beine. 6. Aufsatz. *Ibid.*

1904b. ——. Zur vergl. Morphologie und Systematik der Japydiden. *Ibid.*

1904c. ——. Zur vergl. Morphologie und Systematik der Embiiden. Nova Acta, Bd. 82.
1904. Voss. Ueber den Thorax von Gryllus domesticus Zeit Wiss. Zool., LXXVIII.
1900. Walton. The Basal Segments of the Hexapod Leg. Am. Nat., Vol. XXXIV.
1901. ——. The Metathoracic Pterygoda of the Hexapoda and their Relation to the Wings. Am. Nat., Vol. XXXV.
1830. Westwood. On the Thorax of Insects. Zool. Jour., Vol. V.
1838. ——. On the comparative structure of the Scutellum and other terminal dorsal parts of winged Insects. Entom. Mag., Vol. VI.
1839. ——. Introduction to the Modern Classification of Insects. London.
1889. Wheeler. The Embryology of Blatta germanica and Doryphora decemlineata. Jour. Morph., Vol. III, No. 2.
1893. ——. A Contribution to Insect Embryology. Jour. Morph., Vol. VIII.
1899. Willem. Recherches sur les Collemboles et Thysanoures. Gent.
1862. Winslow. Om byggnaden of Thorax hos Insekterna. Helsingborg.
1879. Wood-Mason. Morphological Notes bearing on the Origin of Insects. Trans. Ent. Soc. London.
1906. Woodworth. The Wing-veins of Insects. Univ. California Agr. Exper. Station Pub. Technical Bull. Entomol., Vol. I, No. I.
1854. Zaddach. Untersuchungen über die Entwickliung und Bau der Gliedertiere. Berlin.

Reference Letters.

—', —", or —'''—Indicates that the sclerite in question belongs to the pro-, meso- or meta-thorax.

—'''', —'''', etc.—Indicates that the sclerite is abdominal.

AD...............Apodeme.
AP...............Apophysis.
C...............Coxa.
C_1...............Eucoxa.
C_2...............Meron.
C_m...............Coximarginal sclerite.
CS...............Cervical sclerites.
CS_1...............Ventral cervicals.
CS_2...............Lateral cervicals.
CS_{2x}...............Posterior lateral cervicals.
CS_3...............Dorsal cervicals.
$C.Pl$...............Cervico-propleuron.
EM...............Epimeron.
EM_c...............Costal sclerite.
EM_a...............Anepimeron.
EM_k...............Katepimeron.
ES...............Episternum.
ES_a...............Anepisternum.
ES_m...............Median region.
ES_k...............Katepisternum.
ES_{kx}...............Katepisternal complex.
F...............Furca.
I...............Intersegmentalia.
I_{pl}...............Prælaterale.
I_{pp}...............Postpleural sclerite.
I_{pt}...............Peritremal sclerites.
L...............Laterale.
L_a...............Anterior laterale.
L_b...............Antecoxal laterale.
L_1...............Episternal laterale.
L_2...............Sternal laterale.
L_3...............Hyposternal laterale.
N...............Notum or tergum.
N_1...............Præscutum.
N_2...............Scutum.

N_2a...............Mediscutum.
N_2b...............Parapsidoscutum (or parapsides).
N_3...............Scutellum.
N_4...............Postscutellum.
N_4a...............Mediophragmite.
N_4b...............Pleurophragmites.
N_4bs...............Superior region of the pleurophragmite.
N_4bi...............Inferior region of the pleurophragmite.
N_4bp...............Pleurophragmal sclerite or parapleuron.
PC...............Complementary coxal plate.
Pl...............Pleuron.
S...............Sternum.
S_1...............Præsternum.
S_2...............Basisternum.
S_3...............Furcisternum.
S_3p...............Pedal region of furcisternum.
S_3pf...............Postfurcal sclerites.
S_4...............Spinisternum.
SP_1, SP_2...............First and second thoracic spiracles.
SP_a...............Abdominal spiracle.
T...............Trochantin or trochantinus.
T_a...............Antecoxal trochantin.
T_b...............Coxal trochantin.
T_1...............Trochantinus major.
T_2...............Trochantinus minor.
TG...............Tegmentary sclerites.
TR...............Trochanter.

EXPLANATION OF PLATES I–IV.

PLATE I.—NEMURA(?). Ventral view of thorax and first two abdominal seg-
ments. Head removed. Legs, abdomen and wings shortened.

PLATE II.—ANISOLABIS and FORFICULA.—Combination figure. Three-quarters
view showing venter, flank, and edge of the dorsum. Head and greater
portion of the legs and abdomen removed. Prothorax based on Anisolabis;
meso- and meta-thorax as in Forficula.

PLATE III.—PERIPLANETA.—Three-quarters view of thorax and first abdominal
segment. Prepared and oriented as fig. XXIII.

PLATE IV.—CARABID LARVA.—Three-quarters view of metathorax and first
two abdominal segments. The sclerite labelled "parapleurite" should be
designated "paratergite."